Warm summers negatively affect duration of activity period and condition of adult stag beetles (*Lucanus cervus*)

M A R K U S   R I N K   and   U L R I C H   S I N S C H   Department Biology, Institute of Integrated Sciences, University of Koblenz-Landau, Koblenz, Germany

Abstract. 1. Three life-history traits of stag beetle imagines were studied in the valley of the River Moselle (Alf, Bullay, Rhineland-Palatinate, Germany): activity period (first observed emergence from the larval habitat until last sighting, 2000–2005), condition (residuals of regression body mass vs. body length, 2003–2005), and dispersal distance (line-of-sight distance between release site and last location, 2003–2005). We used radio telemetry to monitor dispersal of 56 free-ranging individuals and field observations of 266 imagines to estimate the overall duration of the activity period. A total of 330 estimates of conditions were obtained from 171 individuals.

2. The duration of activity period was inversely related to average air temperature during adult activity. In 2003, the activity period lasted 38 days in males and 55 days in females at 21.8 °C air temperature on average; in 2004, 82 days in males and 111 days in females at 17.6 °C.

3. Condition decreased continuously from emergence to death, but the rate of mass loss was 3–4 times greater during the warm summer of 2003 than in the more temperate ones of 2004 and 2005. Replicate measurements in 51 individuals showed that the among-years differences in loss rate were positively related to ambient air temperature during the activity period, but were independent from sex and size.

4. The average dispersal distance was significantly larger in males (802 m) than in females (263 m), but did not differ among the years.

5. The responses of stag beetles to among-years temperature variation suggest that climate change may increase vulnerability of local populations by reducing the activity period and increasing metabolic cost for thermoregulation.

Key words. Climate change, dispersal distance, fitness, life-history traits, *Lucanus cervus*, residual index.

Introduction

Climate change is expected to increase temperature by 1.8–4.0 °C until 2100 and to cause direct and indirect effects in ecology and geographic distribution of many taxa (Walther *et al.*, 2002; Sparks & Menzel, 2002; Root *et al.*, 2003; IPCC, 2007). The actual and future responses of insects have received particular attention, specifically those of pest species which may cause substantial economic harm in agricultural and forest ecosystems (Logan & Powell, 2001; Kiritani, 2006; Musolin, 2007; Logan *et al.*, 2008). The most obvious response is the poleward shift in distribution ranges, as evidenced in but-

terflies and bugs (Parmesan *et al.*, 1999; Musolin & Numata, 2003). Moreover, the onset of spring activity tends to become earlier as evidenced in bugs (Kiritani, 2006). Long-term studies in the UK indicate that the flight period of five aphid species begins about 3–6 days earlier than 25 years ago and that several butterfly species appear about 3 days earlier per decade in spring (Fleming & Tatchell, 1995; Roy & Sparks, 2000). Modification of phenology may enable univoltine bug species to produce an additional generation, as predicted at temperature increases by 2–3 °C (Yamamura & Kiritani, 1998; Musolin & Saulich, 2001). However, the possible implications of global warming for the conservation of currently endangered insect species have not been studied yet.

The saproxylic beetles of woodlands are a group of particular conservation interest, and include the stag beetle *Lucanus cervus* Linnaeus, 1758, one of the most emblematic flagship species of conservation in Europe (Thomaes *et al.*, 2008). Surprisingly little

Correspondence: Ulrich Sinsch, Department Biology, Institute of Integrated Sciences, University of Koblenz-Landau, Universitätsstr. 1, D-56070 Koblenz, Germany. E-mail: sinsch@uni-koblenz.de

is known about its life-history traits which might be sensitive to climate change (e.g. Tochtermann, 1992; Klausnitzer, 1995; Sprecher-Uebersax, 2001; Smith, 2003). Though stag beetles are undoubtly semelparous, neither the exact duration of the subterranean larval stage nor that of the adult activity period have been thoroughly studied. Klausnitzer (1995) and Pratt (2000) mention a larval period of 3–6 years in nature, while a recent study in Germany demonstrated that larval development in enclosures is completed within 3 years (Rink & Sinsch, 2008b). The activity period of adults is thought to be restricted to the warm nights of June and July (Sprecher-Uebersax, 2001; Thomaes *et al.*, 2008), but often dispersing individuals have been observed already in May (Smith, 2003; Rink & Sinsch, 2008a). It is unknown, whether tree sap ingested by adults contributes to longevity and thus increases fitness or not (Bechtle, 1977; Tochtermann, 1992).

As long-term data on the ecology of stag beetle populations are not available yet, our approach to assess potential effects of climate change on life-history traits is to analyse the responses of a local population in Germany to the variation of weather conditions during 3 years, including the exceptionally hot summer of 2003. We consider three life-history traits which are important for the persistence of stag beetle populations and are expected to be sensitive to environmental temperature: (i) duration of activity period, (ii) fitness measured as the condition index, and (iii) dispersal distance. We test the hypothesis that the duration of the adult activity period decreases in warm summers mediated through a faster loss of condition due to increased metabolic rates. If so, reproductive behaviour may be confined to a smaller area around the larval habitat and gene flux among oviposition sites as well as colonisation abilities reduced.

Material and methods

Stag beetles *L. cervus* were studied in the vicinity of the villages Alf and Bullay (Kreis Cochem-Zell, Rhineland-Palatinate, Germany; Rink & Sinsch, 2006, 2007a). Most oviposition sites were located in the shore area of the River Moselle, imagines moved over distances of ca. 2 km at most in an altitudinal range of 94–398 m.a.s.l. (Rink & Sinsch, 2007b). Air temperature 2 m above ground was continuously recorded in Bullay at 180 m.a.s.l., using a meteorological station (ELV, WS 2500).

Activity period of adults

In field, we assessed the beginning of the annual activity period based on the first observation of flying individuals (32 males, 26 females; 2000–2002; details in Rink & Sinsch, 2006) or on the dates of first emergence from nine monitored oviposition sites (117 males, 91 females; 2003–2005; details in Rink & Sinsch, 2008b). Field estimates of the end of adult activity (= death) were obtained from individuals followed using radio telemetry (18 males, 38 females; 2003–2005; details in Rink & Sinsch, 2007a). The exact date of death was verified in radio-tracked specimens dying overground during the up to three location surveys per day. In case of females which stayed in underground shelters, we waited at least 2 days without further movements before checking, if they had lost the transmitter or had died. Therefore, the date of death has an error margin of up to 2 days. Additional data on longevity were collected from beetles (24 males, 20 females, 2000–2005) which were kept in enclosures under near natural conditions and food *ad libitum*.

Condition

All stag beetle imagines collected during the activity periods of 2003–2005 were biometrically processed by measuring body length (distance between the tips of mandible and elytron) using a caliper (to the nearest 0.1 mm) and mass using a digital balance (to the nearest 0.01 g). If an individual was recaptured, size was considered to be the same, but mass was measured again. The same procedure was applied to those imagines which were kept in enclosures yielding individual series of seasonal mass variation. A total of 330 observations were obtained from 171 individuals. Fitness of stag beetles was estimated by calculating the body condition index as the residual of a linear regression of body mass on body length. The residual index has proved to be most reliable condition estimate for arthropods (Jakob *et al.*, 1996; Kotiaho, 1999; Östman *et al.*, 2001; Östman, 2005).

Total dispersal distance

Stag beetles (15–25 per year) were equipped with light-weight radio transmitters (mass: ca. 350 mg, size: 12.5 mm × 6.0 mm × 2.6 mm) and followed up to 21 days (details are given in Rink & Sinsch, 2007a). A Stabo XR 100 scanner equipped with a pre-amplifier PA 15 (Conrad Electronics, Frankfurt, Germany) and either a handheld three-element Yagi-antenna or a telescopic stick antenna was used to locate the individuals at least twice per day. Estimates of the dispersal distance (line-of-sight distance between the release site and the last detected location) were obtained for 35 radio-tracked individuals (14 males, 21 females), which were followed at least three consecutive days and moved more than 5 m from the release site.

Statistical analyses

The influence of single or multiple factors on condition, daily rate of condition loss and on dispersal distance was estimated using linear regression analyses or Multifactor Analyses of Covariance (MANCOVA, type III sum of squares). Categorical factors were sex and study year, while body length (mm), duration of activity period (days), duration of tracking period (days) and environmental temperature (°C) were considered as continuous covariates. Regression models were compared using the conditional sum of squares. Significance level was set to 0.05. Analyses were conducted in Statgraphics Centurion version XV (StatPoint Technologies, Inc., Warrenton, VA, USA).

Results

Life-history trait 1: annual activity period of adults

In the study area, imagines emerged from their larval habitat from mid-May to mid-June. Males emerged significantly earlier (on average 7.1 days) than females of the same site (Fig. 1; *t*-test, $P = 0.048$). The timing of emergence was influenced by temperature (Rink & Sinsch, 2008a), but there was no detectable covariation between the beginning of the annual activity period of males and the spring temperature (linear correlation analysis: $R^2 = 2.4\%$, $P > 0.05$). Thirty-eight out of 49 individuals observed emerging from the larval habitat emerged at 21:00–23:00 hours. Males ($n = 17$, radio telemetry) initiated dispersal flights at 20.45–22.20 hours, whereas females ($n = 15$) left at 21.45–22.45 hours. Field observations of male stag beetles ceased usually at the end of June, though occasionally individuals were seen about a month later. In contrast, females were regularly recorded until mid-July.

In enclosures, males survived usually until early July, but the first individuals died in mid-June. Correspondingly, many females did not die before mid-August, while the first losses occurred in mid-July. Most males died within a few hours without showing previous signs of senility. In contrast, females often stayed almost motionless at the surface several days before death.

The duration of adult activity (period between first and last sighting of imagines) varied considerably among years, but was always lower in males than in females (38 days vs. 55 days in 2003, 82 days vs. 111 days in 2004, 63 days vs. 71 days in 2005). The among-years variation of the activity period corresponded to the variation of air temperature during the activity period (Fig. 2). In 2003, air temperature averaged 21.8 °C (variance: 62.8; range: 7.9–37.7 °C). The activity period of 2004 was the coldest studied (mean: 17.6 °C) with lowest variation of temperatures (variance: 55.2; range:
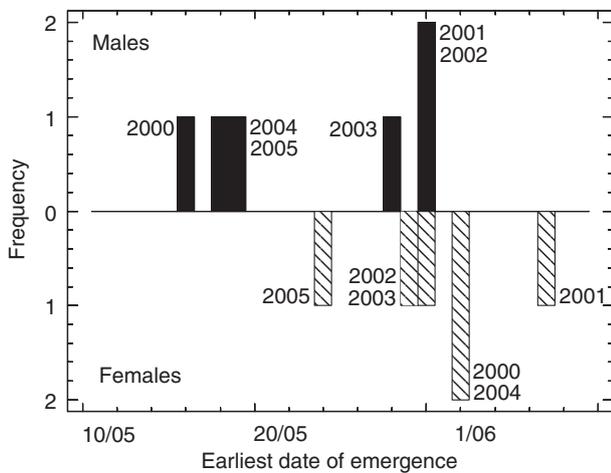
Fig. 2. (a–c) Activity period of adult stag beetles (hatched line) and air temperature variation in the study area. (a) 2003, (b) 2004, (c) 2005. Data are presented as the diel minimum and maximum temperatures measured at 2 m in the shade. Arrows indicate the earliest and latest date at which active males and females were recorded.

0.5–33.2 °C). 2005 resembled 2004 with respect to average temperature (18.5 °C), but day-to-day variation was considerably larger than in 2003 and 2004 (variance: 79.0; range: 1.4–34.6 °C).

Life-history trait 2: seasonal and annual variation of condition

Due to the sexual size and shape dimorphism in stag beetles, sex-specific regression models were calculated to estimate individual condition as the residual index. The linear regression

Fig. 1. Between-years variation (2000–2005) of the date at which the first male and female, respectively, were observed. Numbers at the bars indicate the corresponding year.
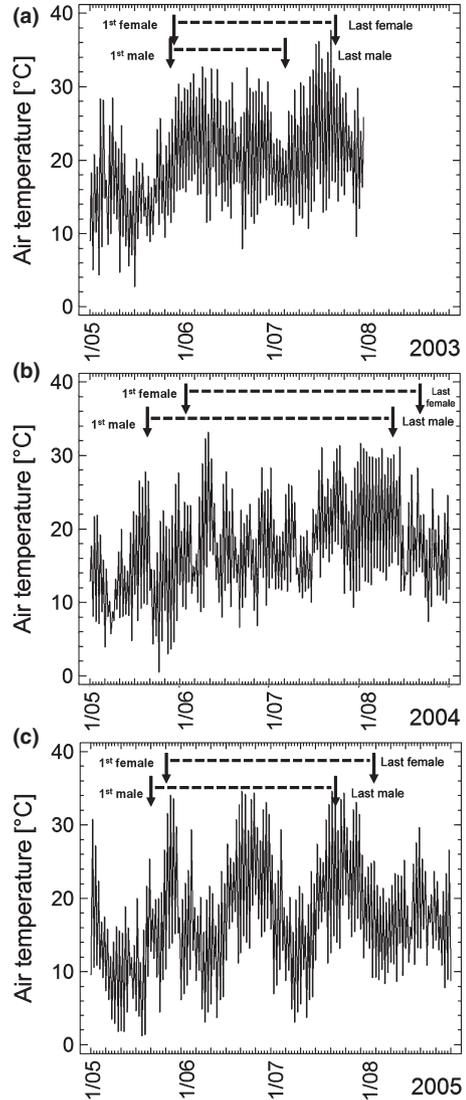
models of individuals captured in field and of those kept in enclosures did not differ significantly in slope and intercept (ANOVA, $P > 0.05$) and were consequently pooled for further analyses. The model for males [mass (g) = $-3.072 + 0.104 *$ length (mm); Fig. 3a] explained 86.15% of mass variation ($r = 0.929$, $F_{1,150} = 940.5$, $P < 0.001$), whereas that for females [mass (g) = $-4.173 + 0.168 *$ length (mm); Fig. 3b] explained 60.22% of mass variation ($r = 0.777$, $F_{1,176} = 269.0$, $P < 0.001$).

Condition decreased significantly during the annual activity period (1 May, arbitrarily assigned as day 1; Fig. 4). Seasonal variation accounted for 37.4% of variance of males condition (multiple regression model: $F = 17.4$, $P < 0.001$), and for 53.8% of females condition ($F = 40.0$, $P < 0.001$). The regression models obtained for the years 2004 and 2005 did not differ significantly in females with respect to slope (2004/2005: -0.011, ANOVA, $P > 0.05$) and to intercept (2004/2005: 0.614, ANOVA, $P > 0.05$), whereas in males slopes (-0.0064) were indistinguishable, but intercepts varied significantly (2004: 0.206, 2005:
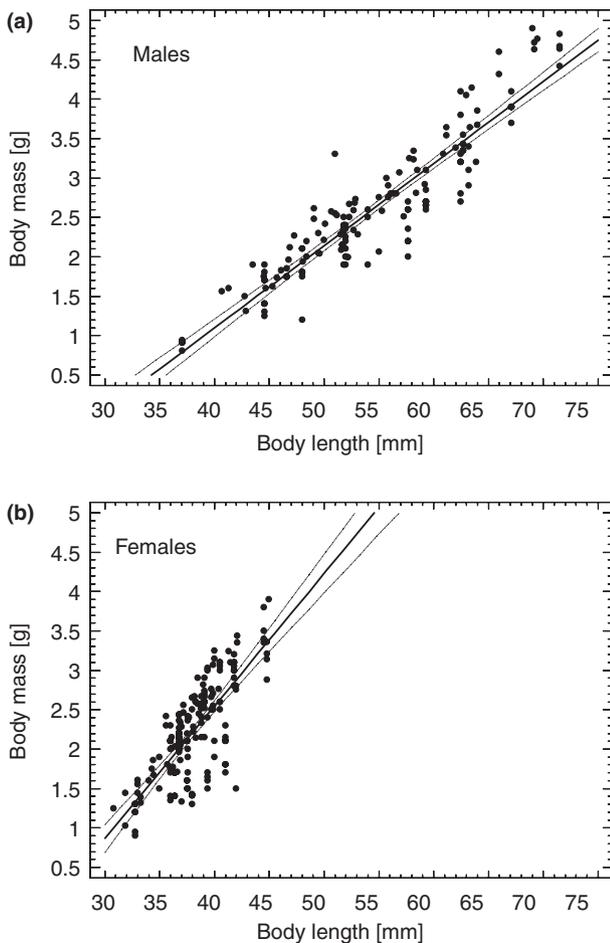
Fig. 4. (a, b) Linear regression models of the condition loss during the activity period of male (a) and female (b) stag beetles. Dots, squares and asterisks represent individual measurements, the bold lines the corresponding regression models of each year. For statistical detail see text.

0.367, ANOVA, $P = 0.005$). In contrast, the models for 2003 had significantly greater slopes (males: -0.025, ANOVA, $P = 0.002$; females: -0.030, ANOVA, $P < 0.001$) and intercepts (males: 1.128, ANOVA, $P > 0.05$; females: 1.459, ANOVA, $P = 0.005$). Thus, the average daily rate of condition loss was 3–4 times greater in 2003 than in the following 2 years.

Replicate estimates (range: 1–10) of condition were obtained in 51 individuals and subsequently, short-term variation of individual condition was related to the corresponding average ambient temperature. Multifactor analysis of covariance revealed that the daily loss rate varied significantly among years (Table 1, MANCOVA, $P = 0.005$; Fig. 5a), but not between males and females (Table 1, MANCOVA, $P > 0.05$). Least square means of loss rate (and corresponding 95% confidence interval) were -0.042 ± 0.011 in 2003, -0.020 ± 0.006 in 2004 and -0.001 ± 0.007 in 2005 (Bonferroni's multiple range test, $P < 0.05$). Among three continuous variables (body length, temperature, day of season) considered, only temperature

Fig. 3. (a, b) Linear regression models of the size–mass relationship in male (a) and female (b) stag beetles. Each dot represents an individual, the bold line the regression model, and the hatched lines the 95% confidence interval. For statistical detail see text.
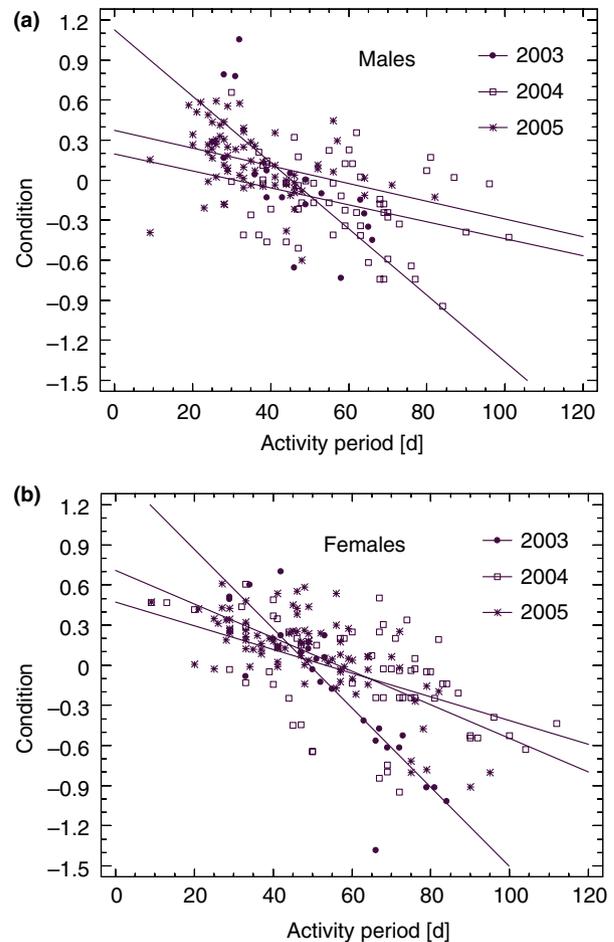
Table 1. MANCOVA of the rate of condition loss (Residuals per day), type III sums of squares.

Source	Sum of squares	d.f.	Mean square	*F*-ratio	*P*-value
Covariates					
Body length	0.00006	1	0.00006	0.03	0.867
Day of season	0.00389	1	0.00389	1.84	0.177
Temperature	0.01688	1	0.01688	7.99	0.005
Main effects					
Year	0.02313	2	0.01156	5.48	0.005
Sex	0.00007	1	0.00007	0.03	0.853
Residual	0.2999	142	0.00212		
Total (corrected)	0.3368	148			
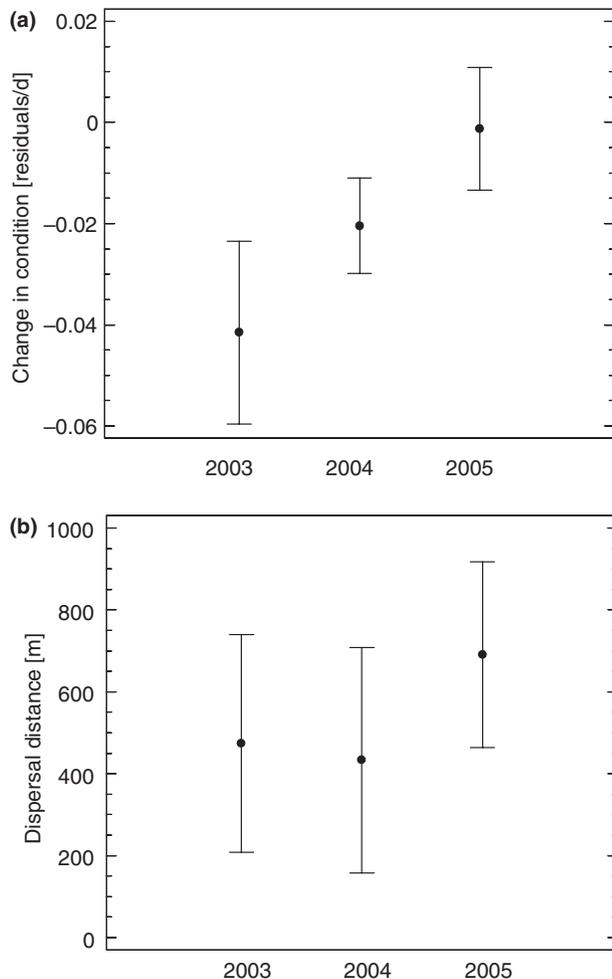
Fig. 5. (a, b) Yearly variation of the change in condition (a), and of the total dispersal distance (b) of adult stag beetles, as calculated by MANCOVA. Each dot represents the arithmetic average, the whiskers the 95% Bonferroni confidence intervals. For statistical details see text and Tables 1 and 2.

covaried significantly with the daily rate of condition loss (Table 1, MANCOVA, *P* = 0.005).

Life-history trait 3: annual variation of dispersal distance

The total dispersal distance achieved by radio-tracked individuals differed significantly between males and females (Table 2, MANCOVA, *P* = 0.003; Fig. 5B), but not among the years (Table 2, MANCOVA, *P* > 0.05). Least square means of annual dispersal distance (and corresponding 95% confidence interval) were 474.2 ± 148.1 m in 2003, 432.9 ± 153.6 m in 2004 and 690.1 ± 153.6 m in 2005 (Bonferroni's multiple range test, *P* > 0.05). In contrast, the least square mean of female dispersal distance (263.0 ± 105.7 m) was considerably smaller than that of males (801.8 ± 123.3 m). The duration of the individual tracking period considered as a covariate did not affect significantly dispersal distance (Table 2, MANCOVA, *P* > 0.05).

Discussion

Empirical evidence of biological responses to climate change requires usually the analysis of data series covering at least 20 years (e.g. Beebee, 1995; Roy & Sparks, 2000; Reading, 2007). Unfortunately, such data series are unavailable for most species and specifically for those of conservation interest. A surrogate approach to predict responses to climate change is to study the effect of current temperature variation within the geographical range due to latitude and altitude, as applied to the Spittlebug *Neophilaenus lineatus* in the UK (Fielding *et al.*, 1999). Climatic warming is expected to expand the length of the oviposition period and to shorten nymphal development in this taxon. Our approach makes use of the natural among-years fluctuation of weather conditions during the activity period of adult stag beetles *L. cervus* in a large population in Germany. The temperature difference between the exceptionally hot summer of 2003 and the cold one of 2004 was about 4 °C, which equals the expected temperature rise until 2100 (Intergovernmental Panel on Climate Change (IPCC), 2007). It seems reasonable to use the observed impacts on life-history traits such as duration of activity (= reproduction) period, condition and dispersal distance to predict potential responses to future climate change.

Table 2. MANCOVA of the dispersal distance (m), type III sums of squares.

Source	Sum of squares	d.f.	Mean square	*F*-ratio	*P*-value
Covariates					
Duration of tracking period	138 414	1	138 414	0.67	0.418
Main effects					
Year	404 162	2	202 081	0.98	0.386
Sex	2 161 800	1	2 161 800	10.54	0.003
Residual	6 155 890	30	205 196		
Total (corrected)	8 583 766	34			

Life-history trait 1: duration of activity period

Our study provides evidence that the length of activity period of adult stag beetles may vary by factor 2 among years in which the exact date of emergence from larval habitats and of death of the last individuals was determined. Comparative data from populations in Switzerland and the UK are unavailable due to differences in the assessment methods (Sprecher-Uebersax, 2001; Smith, 2003; Moretti & Sprecher-Uebersax, 2004). However, two common features of stag beetle phenology arise from these four studies: females emerge later than males, and their activity period is longer than that of males. Timing of emergence during the study period does not show a covariation with temperature, but the absence of statistical significance may be due to the relatively short time series. Nevertheless, the fact that emergence started later in the hot year 2003 than in cooler years corresponds to the trend that stag beetles from south of the Alps emerge later than north of Alps (Moretti & Sprecher-Uebersax, 2004). In contrast, insect with short larval development rather tend to emerge earlier and to produce a second generation per year such as the spruce bark beetle *Ips typographus* (Faccoli, 2009; Jönsson *et al.*, 2009). This may indicate that constraints of larval life-history traits may be the key to the deviating behaviour of stag beetles. The larval development during at least 3 years might buffer temperature extremes in particular years.

The major source of among-years variation in the activity period is probably environmental temperature. However, the observed bisection of duration (2003 vs. 2004) at a temperature increase by only 4 °C on average suggests that increased metabolic costs were not the only cause. A further source of among-years variation may constitute the quality and quantity of food ingested, but no data are presently available to support of this hypothesis.

The superior longevity of females is probably related to the lower metabolic costs for locomotion and to the prolonged stay at and in the oviposition site (Rink & Sinsch, 2007a). Most females performed a single dispersal flight and moved afterwards over short distances on ground to locate a suitable oviposition site, while males flew more frequently and over larger distances. During egg deposition at the last part of the activity period, females stay underground for several days or even weeks which should decrease female mortality due to predation and reduce the metabolic costs due to high diurnal temperatures.

Life-history trait 2: rate of condition loss

A common feature of the activity periods studied was the progressive and linear loss of condition (= a surrogate measure for fitness; Jakob *et al.*, 1996; Kotiaho, 1999) between emergence and death of the beetles, as also observed by Sprecher-Uebersax (2001). Food uptake might have reduced the rate of condition loss, but did not suffice to maintain a given level of condition over a prolonged period, unlike the situation in predatory carabids (Östman *et al.*, 2001; Östman, 2005). The loss rate covaried significantly with ambient temperature and was greatest during the hot summer of 2003. This result sheds a new light on Ant's (1973) observation that male and female stag beetles build small holes in the soil and stay there during hot periods. Ant (1973) related this behaviour to the uptake of moisture, but he published probably the first observation of thermoregulatory behaviour to avoid excessive heating. The hypothesised behavioural thermoregulation agrees with the fact that we never observed flights at temperatures exceeding 26 °C, while ground movements took place at up to 33 °C (Rink & Sinsch, 2007a).

Still, loss rates were lower in 2005 than in 2004, although average temperature was slightly higher in 2005 than in 2004. Thus, magnitude of loss rate cannot be attributed to the average environmental temperature alone. The main difference of the temperature regime in 2005 to those in 2004 and 2003 was that the seasonal variation of temperature was by far greater (Fig. 1). Fluctuating temperatures promote insect growth more efficiently than constant temperature at the same average (Worner, 1992; Ragland & Kingsolver, 2008), and may contribute to reduce condition loss.

Life-history trait 3: dispersal distance

Contrary to the hypothesis that short adult activity period would reduce total dispersal distance, there was no detectable difference among the three thermally rather different study years. All flights of radio-tracked individuals took place within the first 10 days following emergence, i.e. during the usually coldest part of the activity period in May and early June (Rink & Sinsch, 2007a). Since total dispersal distance did not covary with the length of the tracking period either, dispersal by flight seems to represent a burst behaviour during a period in which environmental temperature does not pose limits yet.

Conservation perspectives in a changing climate

Recent studies in Switzerland (Sprecher-Uebersax, 2001), UK (Smith, 2003), Germany (Rink & Sinsch, 2006, 2007a,b, 2008a,b), Belgium (Thomaes *et al.*, 2008), and northern Spain (Galante & Verdú, 2000) indicate that stag beetles are still widely distributed, rather flexible in their oviposition habitat choice and of limited dispersal capacity. The latitudinal range of distribution suggests that neither hot climate (absence in southern Spain and Italy) nor cold climate (absence in northern UK and northern Sweden) are suitable for stable stag beetle populations. In contrast, central European populations seem still frequent and include large number of individuals. Leaving aside conservation issues related to habitat destruction and availability of suitable oviposition sites, this study provides first hints that rising environmental temperature may pose additional threats to the persistence of stag beetle populations.

Stag beetle development consists of a several years lasting larval period and an adult activity period of a few weeks during early summer. Potential impacts of climate change on the duration of the larval development have not been analysed in this or other studies, but individuals raised in captivity completed life cycle within 3 years, the minimum estimate of development in nature (Klausnitzer, 1995; Sprecher-Uebersax, 2001; Rink & Sinsch, 2008b). Captive-bred imagines were smaller than those

from natural larval habitats. If fast development and small adult size are consequences of the warmer thermal regime (winter) during captive breeding, climate change may have similar effects. While a short larval period promotes faster population growth, small-sized females will produce less eggs than large-sized ones (Honěk, 1993) which in turn may lead to a long-term decrease in abundance. This hypothesis will be tested in populations at the southern range of distribution.

Our study suggests that accelerated loss of condition will considerably reduce the duration of the adult activity period at rising environmental temperatures. A temporal compression by up to 50% will have consequences for time budget available for the major adult activities such as dispersal, mating, oviposition, food intake and thermoregulation. Dispersal distance and thus, gene flux among neighbouring oviposition sites will probably remain unaffected. However, the time budget for down-regulating body temperature will augment at cost of the time available for mating, food intake and oviposition – a factor probably contributing to the absence of stag beetles in Southern Spain and Italy. The chance of female/male encounter and mating as a primary consequence of the dispersal flights will probably not be affected, but the reduced time for searching high-quality oviposition habitats may cause females to deposit eggs at less suitable sites because they cannot reach better sites in time. In summary, we predict that global warming will increase the risk of local extinction of stag beetle populations in central and southern Europe due to accelerated loss of fitness and increased costs for thermoregulation.

Acknowledgements

References

Ant, H. (1973) Beobachtungen zur Biologie des Hirschkäfers. *Natur und Heimat*, **33**, 87–92.

Bechtle, W. (1977) Hirschkäfer sind große Süffel. *Kosmos*, **73**, 647–654.

Beebee, T.J.C. (1995) Amphibian breeding and climate. *Nature*, **374**, 219–220.

Faccoli, M. (2009) Effect of weather on *Ips typographus* (Coleoptera Curculionidae) phenology, voltinism, and associated spruce mortality in the southeastern Alps. *Environmental Entomology*, **38**, 307–316.

Fielding, C.A., Whittaker, J.B., Butterfield, J.E.L. & Coulson, J.C. (1999) Predicting responses to climate change: the effect of altitude and latitude on the phenology of the Spittlebug *Neophilaenus lineatus*. *Functional Ecology*, **13** (Suppl. 1), 65–73.

Fleming, R.A. & Tatchell, G.M. (1995) Shifts in flight period of British aphids? *Insects in a Changing Environment* (ed. by R. Harrington and N.E. Stork), pp. 505–508. Academic Press, New York, New York.

Galante, E. & Verdú, J.R. (2000). *Los Artrópodos de la ''Directiva Hábitat'' en España*. Organismo Autónomo de Parques Nacionales, Ministerio de Medio Ambiente, Madrid, Spain.

Honěk, A. (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos*, **66**, 483–492.

Intergovernmental Panel on Climate Change (IPCC) (2007) *Climate Change 2007. The Physical Science Basis. Summary for Policy Makers*, pp. 1–976. Cambridge University Press, Cambridge.

Jakob, E.M., Marshall, S.D. & Uetz, G.W. (1996) Estimating fitness: a comparison of body condition indices. *Oikos*, **77**, 61–67.

Jönsson, A.M., Appelberg, G., Harding, S. & Barring, L. (2009) Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle, Ips typographus. *Global Change Biology*, **15**, 486–499.

Kiritani, K. (2006) Predicting impacts of global warming on population dynamics and distribution of arthropods in Japan. *Population Ecology*, **48**, 5–12.

Klausnitzer, B. (1995). *Die Hirschkäfer*. Westarp Wissenschaften, Die neue Brehm Bücherei, Germany.

Kotiaho, J.S. (1999) Estimating fitness: comparison of body condition indices revisited. *Oikos*, **87**, 399–400.

Logan, J.A. & Powell, J.A. (2001) Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist*, **47**, 160–172.

Logan, J.A., Wolesensky, W. & Joern, A. (2008) Temperature-dependent phenology and predation in arthropod systems. *Ecological Modelling*, **196**, 471–482.

Moretti, M. & Sprecher-Uebersax, E. (2004) 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.

Musolin, D.L. (2007) Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change. *Global Change Biology*, **13**, 1565–1585.

Musolin, D.L. & Numata, H. (2003) Timing of diapause induction and its life-history consequences in *Nezara viridula*; is it costly to expand thedistributin range? *Ecological Entomology*, **28**, 694–703.

Musolin, D.L. & Saulich, A.H. (2001) Environmental control of voltinism of the stinkbug *Graphosoma lineatum* in the forest-steppe zone (Heteroptera: Pentatomidae). *Entomologia Generalis*, **25**, 255–264.

Östman, Ö. (2005) Asynchronous temporal variation among sites in condition of two carabid species. *Ecological Entomology*, **30**, 63–69.

Östman, Ö., Ekbom, B., Bengtsson, J. & Weibull, A.-C. (2001) Landscape complexity and farming practice influence the condition of polyphagous carabid beetles. *Ecological Applications*, **11**, 480–488.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, .J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Pratt, C. (2000) An investigation into the status history of the stag beetle *Lucanus cervus* L. in Sussex. *Coleopterist*, **9**, 75–90.

Ragland, G.J. & Kingsolver, J.G. (2008) The effect of fluctuating temperatures on ectotherm life-history traits: comparisons

among geographic populations of *Wyeomyia smithii*. *Evolutionary Ecology Research*, **10**, 29–44.

Reading, C.J. (2007) Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia*, **151**, 125–131.

Rink, M. & Sinsch, U. (2006) Habitatpräferenzen des Hirschkäfers (*Lucanus cervus*) in der Kulturlandschaft – eine methodenkritische Analyse. *Entomologische Zeitschrift*, **116**, 228–234.

Rink, M. & Sinsch, U. (2007a) Radio-telemetric monitoring of dispersing stag beetles (*Lucanus cervus* L.): implications for conservation. *Journal of Zoology (London)*, **272**, 235–243.

Rink, M. & Sinsch, U. (2007b) Aktuelle Verbreitung des Hirschkäfers (*Lucanus cervus*) im nördlichen Rheinland-Pfalz mit Schwerpunkt Moseltal. *Decheniana*, **160**, 171–178.

Rink, M. & Sinsch, U. (2008a) Geschlechtsspezifisches Fortpflanzungsverhalten des Hirschkäfers (*Lucanus cervus*). *Mainzer Naturwissenschaftliches Archiv*, **46**, 195–210.

Rink, M. & Sinsch, U. (2008b) Bruthabitat und Larvalentwicklung des Hirschkäfers (*Lucanus cervus*). *Entomologische Zeitschrift*, **118**, 229–236.

Roy, D.B. & Sparks, T.H. (2000) Phenology of British butterflies and climate change. *Global Change Biology*, **6**, 407–416.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Smith, M.N. (2003) *National Stag Beetle Survey 2002*. People's Trust for Endangered Species, London.

Sparks, T.H. & Menzel, A. (2002) Observed changes in season: an overview. *International Journal of Climatology*, **22**, 1715–1725.

Sprecher-Uebersax, E. (2001). *Studien zur Biologie und Phänologie des Hirschkäfers im Raum Basel, mit Empfehlungen von Schutzmassnahmen zur Erhaltung und Förderung des Bestandes in der Region (Coleoptera: Lucanidae, Lucanus Cervus L.)*. PhD Thesis, University of Basel, Switzerland.

Thomaes, A., Kervyn, T. & Maes, D. (2008) Applying species distribution modelling for the conservation of the threatened saproxylic Stag Beetle (*Lucanus cervus*). *Biological Conservation*, **141**, 1400–1410.

Tochtermann, E. (1992) Neue biologische Fakten und Problematik der Hirschkäferförderung. *Allgemeine Forstzeitschrift*, **47**, 308–311.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Worner, S.P. (1992) Performance of phenological models under variable temperature regimes – consequences of the Kaufmann or rate summation effect. *Environmental Entomology*, **21**, 689–699.

Yamamura, K. & Kiritani, K. (1998) A simple method to estimate the potential increase in the number of generations under global warming in temperate zone. *Applied Entomology and Zoology*, **33**, 289–298.