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Differences in male:female ratio among species of the genus *Carabus* L. (Coleoptera: Carabidae) in south Sweden

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The male:female (sex) ratio is of considerable importance in understanding population dynamics of species. A null hypothesis was tested that the male:female (sex) ratio of *Carabus* species does not differ measurably when entire seasons are considered, but may differ considerably over shorter periods, indicating differences in annual rhythms between the sexes. The sex ratios in nine *Carabus* species (*C. arvensis, C. cancellatus, C. coriaceus, C. glabratus, C. granulatus, C. hortensis, C. nemoralis, C. nitens*, and *C. violaceus*) were studied using pitfall traps in forests and open land, totally 20 sites, during the entire seasons of 2007, 2009, and/or 2011. The ratio varied considerably and mostly consistently among species. The ratios were < 1 (usually ca 0.6), calculated over entire seasons in *C. arvensis, C. glabratus* and *C. granulatus*. On the contrary, males dominated in the other six species, and were particularly over-represented in *C. cancellatus, C. nemoralis*, and *C. nitens* with ratios of 2.2–2.7. Differences in the male:female ratio between different parts of seasons were demonstrated in three species. Calculated over entire seasons, there was some dominance of males in *C. coriaceus* and *C. hortensis*. Females dominated over males in July, males dominated in September. The pattern for *C. violaceus* was less consistent. The possible influence on the sex ratios of capturing method, habitat properties, nutritional status, season, differing life span and annual or diurnal rhythm of activity of males and females is considered and discussed.

Keywords: ground beetles, sex ratio, male:female ratio, forest, grassland, heath, habitat, variability

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INTRODUCTION

The male:female (sex) ratio is of considerable importance in understanding population dynamics of species. The ecology and taxonomy of carabids, in particular the *Carabus* Linnaeus, 1758 species, have attracted considerable attention among entomologists. Several large monographs on *Carabus* of the world (Imura & Mizusawa 1996; Deuve 2004) or parts of the world (e.g., Turin et al. 2003) have been published during the last two decades, and the number of species described increases from year to year. Even though the ecology of many *Carabus* species, particularly in Europe and Japan, is rather well known, little direct attention has been di-

rected towards describing and clarifying variability in the proportions of males to females over entire seasons. Field entomologists studying *Carabus* species for other purposes often get the impression that the proportion of males to females (sex ratio) seems to vary considerably and consistently among species and sites, at least over shorter periods of time.

It is quite difficult or impossible, especially in forest habitats, to count or even estimate the number of *Carabus* individuals in a reliable way. A far-reaching demolition of considerable areas of ground would be necessary. Therefore, pitfall trapping is the most common method to obtain information, though it should be emphasised that such methods actually rather measure "activity abundance", a function of both abundance and activity.

The main studies on sex ratios in *Carabus* species were published by Szyszko and co-workers (e.g., Szyszko 1977; Szyszko et al. 2004), at least partly using pitfall trapping, as in my study. They demonstrated that habitat properties are of importance to the male:female ratio of some species, with males dominating over females in more fertile environments. My own field observations seem to indicate, that there are consistent differences in the sex ratio also between *Carabus* species within the same habitat and site. The clear dominance of females during entire seasons in some species, a dominance of males in others, is difficult to explain from a population ecological point of view, as males have no real biological function when females are absent or inactive. Several species from various habitats in the same geographical area have to be studied in this respect to get a more detailed account of the validity of this problem.

The aims of this paper are to describe and discuss the sex ratio of nine *Carabus* species, originating from pitfall trapping in forest, grassland and heath habitats, totally twenty sites, in Scania, south Sweden. These *Carabus* species are all those possible to find in numbers in this province. My null hypothesis is that no or only slight differences exist, measured over entire seasons, in the sex ratio of *Carabus* species. However, measurable or considerable differences may exist over shorter periods of time, indicating variability in annual rhythms of males and females. The potential influence of habitat type, season, duration of sampling period, and annual or diurnal rhythm of activity of males and females, will be considered or discussed. The study is based on individuals captured quantitatively during entire seasons.

MATERIALS AND METHODS

Carabus individuals were sampled quantitatively using pitfall traps over two entire seasons, 2007, 2009, and/or 2011. Habitats studied were forests, heaths, and grasslands in various parts of the province of Scania, south Sweden. The climate of this area is temperate, suboceanic and subhumid. Mean precipitation figures range 500 to 800 mm y^{-1}, mean temperature of the coldest month 0 to –2 °C, of the warmest month 16 to 17 °C. *Carabus* species may be active on the soil surface in this area at most from early April until early October, though usually over a shorter period of the season, with considerable and consistent differences among species.

Cylindrical pitfall traps, length 100 mm, diameter 75 or 87 mm, with a very smooth, glossy surface were installed along transects at an equidistance of 5 or 10 m, 10-20 traps in each of the twenty sites considered. The traps were emptied twice, sometimes once, a week, and no preservative was used in the traps. All individuals sampled were determined to species and sex. Nine species (out of eleven species found) were abundant enough to render sex ratio calculations meaningful.

Six species, *Carabus coriaceus* Linnaeus, 1758, *C. glabratus* Paykull, 1790, *C. granulatus* Linnaeus, 1758, *C. hortensis* Linnaeus, 1758, *C. nemoralis* O.F. Müller, 1764, and *C. violaceus* Linnaeus, 1758 were sampled from early April to the end of September in ten beech (*Fagus sylvatica* L.) forests, beech being the native forest-forming tree species on not too bad-drained ground in the region. Five of these sites were

developed on Podzols from gneiss or sandstone moraine and were almost devoid of any forest-floor vegetation. The other five beech forests grew on Cambisol soils on moraines with a higher clay content and lower soil acidity with a rich forest floor of herbaceous plants and some shrubs. The remaining three species, *C. arvensis* Herbst, 1784 (=*arcensis* sensu auct.), *C. cancellatus* Illiger, 1798, and *C. nitens* Linnaeus, 1758 were sampled in other habitats; *C. arvensis* in four heath sites on gneiss moraine, dominated by *Calluna vulgaris* L. and some acidicolous grasses, and in three pine forest sites on sand. *C. cancellatus* was sampled in three grassland sites on sand, and *C. nitens* in one of these grassland sites (not found in numbers anywhere else).

Significance level of difference between mean number of males and females captured per site in a particular month or during entire seasons was calculated using t-test for small samples according to Bailey (1969, 5th impression, p. 48). As the male:female data in all species did not deviate appreciably between the two sampling years, they were treated together in order to obtain a larger material for analysis.

RESULTS

The sex ratio of the nine *Carabus* species studied varied considerably and mostly consistently among species (Table 1-2). The ratios of *C. arvensis, C. glabratus* and *C. granulatus* were < 1 (mostly ca 0.6) in all sites, calculated throughout entire seasons. These species are mainly spring–early summer breeders. On the contrary, males dominated over the entire seasons in the other six species, and were particularly over-represented in the catches of *C. cancellatus, C. nemoralis, and C. nitens* with sex ratios of 2.2–2.7. The most common of these species, *C. nemoralis,* is an early spring breeder. It had a decided frequency maximum already in April in the five beech forest sites on Cambisols; as many as 76 % of all individuals captured were found in April. The sex ratio was as high as 4.3 during this month (Table 1) In the less frequent catches of this species later during the seasons, females actually dominated (July) or the ratio was close to 1 (September), a fact that only contributed to a small reduction in the overall ratio of this species. Out of the 149 individuals of *C. cancellatus* caught in the three grassland sites, 104 individuals were males and the sex ratio thus 2.3 (Table 2). This species is usually almost absent in pitfall catches later in the season. A similar ratio (2.2) was found in the less common *C. nitens* (Table 2). This species is usually not at all found in late summer and autumn pitfall catches in south Sweden.

A more diversified pattern of the sex ratio is demonstrated for *C. coriaceus, C. hortensis* and *C. violaceus*, abundant woodland species of this region. Calculated over entire seasons, there was some dominance of males, most markedly (sex ratio 1.57) in *C. violaceus* (Table 1). These species are all summer or early autumn breeders, not occurring in larger numbers until June or early July. Out of the 22 individuals of *C. hortensis* captured already in April, 20 were females. Females also dominated over males (sex ratio 0.68-0.82) among the totally 419 individuals caught in July in the ten beech forest sites, whereas males dominated (sex ratio 1.47-1.52) among the 953 individuals from September, when the frequency of this species peaked (Table 1). A rather similar pattern was displayed by *C. coriaceus*, at least in the Cambisol beech forest sites, where it was quite abundant in summer and autumn. The sex ratio averaged 0.70 in July, but increased to 2.24 in September, when the abundance of this species culminated. The pattern for *C. violaceus* was less consistent, but males dominated the catches in July, when this species was most frequent.

DISCUSSION

In addition to interspecies differences, the sex ratio of carabids may or might be influenced by several other conditions, as indicated in the introduction. Habitat fertility, though difficult to define or characterise from a carabid point of view, may influence the sex ratio. In studying *C. arvensis* in various forest habitats in Poland, Szyszko (1977) demonstrated that males domi-

Table 1. Influence of season and type of site on male:female ratio. Mean *Carabus* captures calculated for April, July, and September in ten beech forest sites on contrasting soils (five sites on Podzol, five on Cambisol) in the province of Scania, south Sweden. Total number of individuals found, male:female ratio, and significance (p-level) of mean difference between number of males and females.(n.s.= $p>0.05$; not cal.= not calculated because only one site or too few individuals). Significance (p-level) of difference between mean number of males and females captured per site in a particular month or during entire seasons calculated using t-test for small samples according to Bailey (1969, 5th impression, p. 48). As the data for all species and months did not deviate appreciably between the two sampling years, they were treated together in order to obtain a larger material for analysis. *C. glabratus* is almost exclusively found on Podzols, *C.granulatus* on Cambisols.

Species	Soil type	Number of sites	Month	Number of individuals	Male:female ratio	p-level
C. coriaceus	Podzol	5	April	0	-	not cal.
			July	21	1.3	n.s
			Sept	86	1.5	<0.05
	Cambisol	5	April	2	-	not cal.
			July	256	0.70	<0.001
			Sept	376	2.24	<0.001
	Both types	10	Apr–Sept	741	1.38	<0.001
C. glabratus	Podzol	5	April	0	-	not cal.
			July	112	0.62	<0.01
			Sept	7	-	not cal.
			Apr–Sept	119	0.61	<0.01
C. granulatus	Cambisol	5	Apr–Sept	44	0.52	<0.01
C. hortensis	Podzol	5	April	22	0.10	<0.001
			July	217	0.82	<0.01
			Sept	588	1.52	<0.001
	Cambisol	5	April	2	-	not cal.
			July	202	0.68	<0.01
			Sept.	365	1.47	<0.01
	Both types	10	Apr–Sept	1396	1.77	<0.05
C. nemoralis	Podzol	5	Apr–Sept	37	1.85	<0.01
	Cambisol	5	April	437	4.27	<0.001
			July	51	0.60	<0.05
			Sept	69	1.03	n.s
	Both types	10	Apr-Sept	594	2.67	<0.001
C. violaceus	Podzol	5	April	3	-	not.cal.
			July	148	2.36	<0.001
			Sept	45	0.80	n.s.
	Cambisol	5	April	0	-	not cal.
			July	61	1.10	<0.001
			Sept	18	-	not cal.
	Both types	10	Apr–Sept	275	1.57	<0.01

nated in more fertile forests, females in poor forest sites. A hypothesis was proposed that the sex ratio could be utilised as an index of fertility of a forest site. Originating from this hypothesis, the *Calluna vulgaris* heath sites of my study would all be less fertile, which seems quite likely. However, this did not seem to be the case with the three *Pinus* forest sites studied (Table 2), when considering the apparently rich occurrence of probably suitable prey animals.

However, degree of satiation may influence the mobility (and thereby pitfall catches of males relative to females). The locomotory activity of satiated females of *C. hortensis* was lower than of satiated males in beech and pine forests studied by Szyszko et al. (2004), whereas hungry males and females had a similar degree of activity. They concluded that the more males in pifall catches in relation to females, the better the food situation in the forest.

Sexual attraction of males by females may also influence results of pitfall trapping studies (Baumgartner 2000). Females captured may attract more males than randomly. However, the very many times each trap was emptied during a season would have counteracted such effects. And male:female ratios significantly <1, as found in several species (Tables 1-2), cannot be explained this way.

Seasonal activity of carabids may differ considerably among species even in the same habitat and site. Out of the *Carabus* species treated in this study, *C. nemoralis, C. granulatus, C. cancellatus, C. arvensis* and *C. nitens* are spring–early summer breeders, whereas *C. coriaceus, C. hortensis, C. violaceus,* and *C. glabratus* are late summer–autumn breeders in south Scandinavia. These differences in annual rhythms will influence the relative and absolute frequencies over the season. It could be expected that males and females are active almost simultaneously and the sex ratios thus constant. However, results of this study clearly show that this is mostly not the case. In *C. hortensis* and *C. coriaceus*, the two most frequent species of this study, females were

Table 2. Influence of season and type of site on male:female ratio of *Carabus cancellatus* and *C. nitens* in treeless grasslands, and of *C. arvensis* in *Calluna* heaths and *Pinus* forests. Total number of individuals found, male:female ratio, and significance (p-level) of mean difference between number of males and females; not cal.= not calculated because only one site studied. None of the species were found in the September catches. Statistical methods used as in Table 1.

Species	Soil type	Number of sites	Month	Number of individuals	Male:female ratio	p-level
C. arvensis	Heathland on moraine	4	Apr–May	81	0.65	<0.05
			June-July	71	0.73	<0.05
			Apr–July	152	0.69	<0.01
	Pine forest	3	Apr-July	77	0.51	<0.01
C. cancellatus	Grassland on sand	3	Apr–June	124	2.3	<0.001
			July-Aug	25	2.6	<0.05
			Apr-Aug	149	2.31	<0.001
C. nitens	Grassland on sand	1	Apr-Aug	26	2.2	not cal.

overrepresented in the catches of July, males in the catches of September.

Differences in sex ratios over the season have been demonstrated also for other carabids by pitfall trapping. The sex ratio varied with season in several forest carabids in France. Males were more numerous in spring and females in autumn (Benest & Cancela da Fonseca 1980). In Danish farmland, the sex ratio of *Agonum dorsale* was generally low and decreased from 0.43 in spring to 0.23 in the summer (Jensen et al.1989). The sex ratio increased in the spring-breeding *Poecilus cupreus* towards the end of the activity period in Swedish wheat fields (Ericson 1978). In a Belgian study, the sex ratio was in favour of males in *Trechus obtusus* in the beginning of the reproductive season, but later on there was a dominance of females (Desender et al. 1980). In the subarctic forests of northern Finland, males of *C. glabratus* occurred during a shorter period than females, thus influencing the sex ratio during the brief season of this region (Vainikainen et al. 1998). These and other observations of sex ratio variability over the season seem to indicate that such differences might be species specific, though probably influenced by site properties and climatic conditions as well.

Habitat dynamics of various types have been reported to influence the sex ratio of carabids. The appearance of new ground may be of importance. When colonising recently available ground, the sex ratio of *Carabus cumanus* and *Carabus exaratus* changed measurably (Knysh & Zamotailov 2005). This would favour initial colonisation by that sex which has the best power of dispersal and consequently influence the sex ratio. Experiments have shown that some *Carabus* species are able to move several hundred m d^{-1} in the same direction (Turin et al. 2003). Females of *Carabus problematicus* tended to disperse more frequently than males in a study from the Netherlands (Rijnsdorp 1980). Though sometimes influenced by tree harvesting, forests generally constitute more stable habitats that heaths and grasslands, which are secondary ecosystems in this part of the world. Differences between sexes in life span have occasionally been reported in *Carabus*, conditions that could influence the sex ratio of imagines. However, it does not seem likely that more than a small share of the imagines may survive to the age of four years. Only one male of *C. glabratus* was re-captured after three years in subarctic Finland (Vainikainen et al. 1998). Climate (altitude above sea-level) influences the life span of *C. problematicus* in Britain. The life cycle of females was predominantly annual at low altitude, being biannual at high altitudes. The life cycle of males was mainly annual over the entire altitude range studied (Butterfield 1986). Some females of this species reproduce for at least two seasons in the Netherlands (Rijnsdorp 1980). According to Baumgartner et.al. (1997) *Carabus auronitens* may survive much longer, even until the 5^{th} season. There is, however, no information about mean differences in longevity between males and females of *Carabus* species under field conditions. That difference in average life span between males and females would be of any great importance to the sex ratios measured in *Carabus* species seems unlikely.

Capturing methods used to determine sex ratios might influence the results. Pitfall trapping offers a measure of "activity abundance" (cf. Introduction) of carabid beetles rather than an absolute measure of carabid numbers per unit area. Philip & Burgess (2008) demonstrated that more *Ctenognathus novaezelandiae* males were caught by searching the forest floor litter, while females dominated in pitfall trapping. A general bias could therefore be caused by differences in mobility between males and females. However, it seems unlikely to me, that the considerable differences in sex ratios between related species of *Carabus*, as demonstrated in my study, could mainly be explained by such a bias. If this is true, great differences in mobility of males and females have to exist between taxonomically related species.

Whether differences in diurnal activity may influence the sex ratio recorded by pitfall trapping is little known, and does not seem likely. All species

studied are to a large extent night-active (Thiele & Weber 1968), with only limited activity during day-time. Day-time activity might partly be a sign of disturbance, but *C. cancellatus* was reported to have diurnal activity during the reproductive period (Weber 1966). Latitudinal differences between various parts of the distributional range may influence the diurnal activity pattern. *C. glabratus* and *C. violaceus* populations of central Europe are predominantly night-active, but these species are also active during the day in northern Scandinavia, with less differences in light between days and nights (Thiele & Weber 1968).

CONCLUSIONS

It is apparent from the results reported from pitfall trapping that the sex ratio of *Carabus* imagines is far from constant, and consistently far from 1.0 in several species, even when entire seasons and the same sites are considered. So far, the null hypothesis of my study has to be rejected. This may be due to original differences in the number of males and females developed to imago stage, rather than to differences in length of the active and inactive periods between males and females, or to differences in life duration, as discussed above. It also seems unlikely that biases caused by the capuring method could have caused these differences, though it should be kept in mind that results represent "activity abundance" of males and females. The over-representation in the autumn of males of the late-breeding *C. coriaceus* and *C. hortensis* and the great over-representation of males early in the season of the spring breeding *C. nemoralis* is difficult to explain from an ecological point of view. Food resources would be better utilized, if males went into inactivity when not "needed" any more, or stayed inactive in the spring until enough females appeared, respectively. The consistently high sex ratio in *C. cancellatus* and the consistently low ratio in *C. arvensis* and *C. glabratus* are other matters of concern. It seems unlikely, that males of *C. arvensis* and *C. glabratus* would be much less active than females in just these species, whereas the opposite condition would be valid in *C. cancellatus*. Much fewer active males relative to females of the two former species, compared to the last-mentioned one, seem necessary to keep their populations at an appropriate level.

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