Life cycles in the ground-beetle tribe Pogonini (Coleoptera, Carabidae) from the Lake Elton region, Russia

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ABSTRACT

In 2006-2007, the main features of life cycles in seven species of the tirbe Pogonini in the semi-desert Lake Elton region, Russia were studied. Six species, *Cardiaderus chloroticus*, *Pogonus transfuga*, *P. meridianalis*, *Pogonistes rufoaeneus*, *P. angustus* and *P. convexicollis*, are spring breeders. Among them, *P. transfuga*, *P. meridionalis* and *P. rufoaeneus* are iteroparous while *C. chloroticus*, *P. angustus* and *P. convexicollis* are semelparous. The life cycles of all these species are monovariant monovoltine with spring or spring-summer reproduction and adult (immature or both immature and spent) hibernation. However, the life cycle in *C. chloroticus* is possibly bivoltine. In contrast, *P. cumanus* is an autumn-breeding iteroparous species, its life cycle being monovariant monovoltine with obligate larval hibernation and obligate adult aestivation, parapause. This is a surprising finding, because previously all Pogonini were considered to be "spring breeders" or "imaginal hibernators". Among the species studied, *P. transfuga* and *P. meridionalis* can be characterized as halophiles, because they live in habitats with moderate salinity. All the other species are pronounced halobionts because, with rare exceptions only, they are restricted to high-salinity habitats. Parasitic mites of the family Podapolipidae were found on *P. transfuga*, *P. meridionalis*, *P. cumanus* and *P. rufoaeneus* adults. Survival over winter and reproduction during a second season, together with the new generation specimens, is an important precondition for dispersal of Podapolipidae. On the other hand, this greatly restricts the range of their possible hosts.

Keywords: Carabidae, Pogonini, Podapolipidae, life cycle, population, spatial and temporal distribution, semi-desert zone, desert steppe, Western Palaearctic

INTRODUCTION

The carabid beetle tribe Pogonini is widespread and, according to different estimates, contains between 77 and 100 species worldwide (Kryzhanovsky, 1982; Lorenz, 1998). Of these, 56 species live in the Palaearctic region (Bousquet, 2003). Salinity tolerance is a major physiological characteristic of all Pogonini species (Heydemann, 1962) which allows them to live in habitats of variable salinity, ranging from the banks of brackish-water ponds, streams and rivers to marine coasts and even virtually lifeless salinas. The biology of most of the Pogonini species is still not clearly understood because, as a rule, only a few, irregular and short-term observations have been reported for these beetles. Furthermore, the species of some genera, e.g. *Cardiaderus* Dejean, 1828, *Diodercarus* Lutshnik, 1931, *Olegius* Komarov, 1996, *Sirdenus* Chaudoir, 1971, are cryptobionts, which are never abundant, and so their records are a matter of luck, as a rule.

Larvae have only been described for ten species from three genera of Palaearctic Pogonini (Jeannel, 1941; van Emden, 1942; Sharova, 1958, 1964; Larsson, 1968; Raynaud, 1976; Luff, 1985, 1993; Arndt, 1991; Grebennikov & Bousquet, 1999), and their population dynamics are effectively terra incognita. Detailed information concerning seasonal activity and habitat requirements are only available for four species of *Pogonus* Dejean, 1821: *P. chalceus* (Marsham, 1802), *P. transfuga* Chaudoir, 1870, *P. litoralis* (Duftschmid, 1812) and *P. luridipennis* (Germar, 1823) (Larsson, 1939; Paarmann, 1976; Desender, 2000; Turin, 2000; Matalin & Makarov, 2006). The reproductive cycle, geographic distribution and habitat requirements have been thoroughly studied in the first two species (Paarmann, 1976, 1979; Desender, 1985, 2000; Matalin & Makarov, 2006), and the development under laboratory conditions has been observed in the third species (Nekuliseanu, 1990).

MATERIAL AND METHODS

Vegetation

Carabid beetle communities on the banks of Lake Elton, Volgograd Region, Russia, were studied from 10 May until 31 October 2006, and from 1 April until 10 May 2007. The area is located near the Russia-Kazakhstan border (49°12.47'N, 46°39.75'E).

Lake Elton is situated inside the blind drainage Botkul-Bulukhta desert depression, which has a strongly pronounced salt-dome structure. Desert steppes are typical plant associations in most of the habitats there (Safronova, 2006). The most abundant plants in this landscape are *Artemisia lerchiana*, *A. pauciflora*, *A. austriaca*, *Kochia prostrata*, *Agropyron desertorum* and *Festuca valesiaca*. On salinas in floodplain terraces and in lakeside salt-marshes, hyper-halophilic communities are formed, where *Halocnemum strobilaceum*, *Atriplex cana*, *Anabasis salsa*, *Salicornia europaea*, *Salsola collina*, *S. tragus*, as well as *Artemisia santonicum*, *A. pauciflora*, *Suaeda physophora*, *Limonium suffruticosum*, *L. caspium* and *L. gmelinii*, are dominants. Dense reedbeds grow in river valleys.

Trapping

During both years, beetles were collected in three habitats: a lakeside salt-marsh, a salina on a floodplain terrace of the Khara River, and reedbeds along the right bank of the Khara River (Fig. 1).

Fig. 1. Locations of study habitats in the Lake Elton region.
A-B – lakeside salt-marsh; C-D – salina on a floodplain terrace of the Khara River; E-F – reedbeds along the Khara River; A, C, E – spring (late April – early May); B, D, F – summer (late July – early August).

Plastic pitfall traps of 0.5 l capacity and 72 mm upper diameter with 4% formalin as a fixative were used for collecting. In each habitat, traps were arranged along a transect at 10 m intervals. The traps were checked at 10 day intervals on the 10th, 20th and 30th (31st) of each month. The traps were maintained from November 1st, 2006 until of March 31st.

Material

During the trapping period, 12 species of Pogonini were collected, of which seven were abundant: *Cardiaderus chloroticus* (Fischer-Waldheim, 1823) – 73 ex., *Pogonus transfuga* Chaudoir, 1870 – 2,175 ex., *P. meridianalis* Dejan, 1828 – 142 ex., *P. cumanus* Lutshnik, 1916 – 77 ex., *Pogonistes rufoaeneus* (Dejean, 1828) – 107 ex., *P. angustus* (Gebler, 1830) – 29 ex. and *P. convexicollis* Chaudoir, 1871 – 47 ex. (Table 1).

Data analysis

Each specimen was dissected and the sex and age determined using a modified version of the method of Wallin (1987). Six physiological states in the adults of both sexes were distinguished, based on gonad conditions: teneral, immature, mature of either the first or second year and spent of either the first or second year of life. As additional criteria, the condition of the mandibles (Butterfield, 1986), as well as the surface of the pronotum and elytra, were evaluated. In females, the number of ripe eggs in the ovaries was estimated. Moreover, in each beetle the conditions of the hind-wings (den Boer, 1977) and wing muscles (i.e. dorso-ventral mesothoracal) (Tietze, 1963; Matalin, 1997b) were recorded, followed by the calculation of the index of potential migrants, *Ipm* (Matalin, 2003). Finally, the rate of infestation by parasites of each beetle was determined. Because data on the duration of development of pre-imaginal stages and number of eggs were not normally distributed, the differences between the median values were tested using Mann-Whitney U-test for independent n (Borovikov, 2001).

RESULTS

Activity and life cycles

The seasonal activities of all studied species were characterized by high fluctuations. In habitats with periodic floods (salina on a floodplain terrace and reedbeds) the pattern of activity in *P. transfuga* and *P. meridionalis* was more smooth, albeit sometimes sizeable amplitudes of population curves. In habitats with casual floods (lakeside salt-marsh), the abundances of all *Pogonistes* spp. and, especially, *C. chloroticus,* changed rapidly every

Table 1. Seasonal changes in demographic population structure of seven Pogonini species in three study habitats in the Lake Elton region.

Habitats	Species	Stage	2006																	2007			
			May		June			July			Aug			Sept			Oct			April			May
			20	31	10	20	30	10	20	31	10	20	31	10	20	30	10	20	31	10	20	30	10
Lakeside salt-marsh	Cardiaderus chloroticus	teneral																					
		immature	/2	/1			1/		1/	1/2		4/3							/1	6/	/1		
		mature	1/2	2/1	1/1			1/	1/	2/		2/	1/	1/							25/4		1/
		spent			/1						1/					1/2							
		Total	**1/4**	**2/2**	**1/2**		**1/**		**2/**	**3/2**		**7/3**	**1/**	**1/**		**1/2**			**/1**	**6/**	**25/5**		**1/**
	Pogonistes angustus	teneral																					
		immature					/1	3/7		3/		/2	/2	1/3	/1	1/	/2						
		mature								/2				1/									
		spent																					
		Total					**/1**	**3/7**		**3/2**		**/2**	**/2**	**2/3**	**/1**	**1/**	**/2**						
	Pogonistes rufoaeneus	teneral							/2	1/													
		immature	/2	/4				/1	/1	/3	1/	/1	1/2	/1	1/	1/	/1	/1		1/5	/2	/2	/2
		mature	9/5	3/1	3/2	4/			/2	1/			2/	3/	1/1	1/1					3/1		8/4
		spent P					/2		/3			2/1	4/2										
		spent A		/1	1/																		
		Total	**9/7**	**3/6**	**4/2**	**4/**	**/2**	**/1**	**/8**	**2/3**	**1/**	**2/2**	**7/4**	**3/1**	**2/1**	**2/1**	**/1**	**1/1**		**1/5**	**3/3**	**/2**	**8/6**
	Pogonistes convexicollis	Teneral				1/			2/				/1	/1									
		immature										/2	1/										
		mature	5/5	8/	3/1	1/1									1/			1/1			2/	/1	
		spent							/1				1/1										
		Total	**5/5**	**8/**	**3/1**	**2/1**			**2/1**			**/2**	**2/2**	**/1**	**1/**			**1/1**			**2/**	**/1**	
	Pogonus cumanus	teneral		/1					/1														
		immature								1/2	/1			1/1	/1								
		mature P									3/4		17/11	17/9	5/1			1/					
		mature A	1/	1/	1/																2/	/1	1/
		spent P														/2	2/1	1/					
		spent A	/1	/1							/1			/1							/1	/1	
		Total	**1/1**	**1/2**	**2/1**				**/1**	**1/2**	**3/6**	**1/1**	**17/20**	**18/11**	**5/2**	**/2**	**2/1**	**2/**			**2/1**	**/1**	**1/**

Habitats	Species	Years	2006																	2007			
		Months	May		June			July			August			September			October			April			May
		Days	20	31	10	20	30	10	20	31	10	20	31	10	20	30	10	20	31	10	20	30	10
Salina on a floodplain terrace	*Pogonus meridionalis*	teneral											2/										
		immature					1/						1/1	1/									/1
		mature P	15/7	23/8	14/9	2/4	3/	1/2					1/							4/2	9/7		5/5
		mature A																			3/		½
		spent					1/2	/2					/1	1/			1/			1/			
		Total	**15/7**	**23/8**	**14/9**	**2/4**	**5/2**	**1/5**					**5/1**	**1/**			**5/2**			**5/2**	**12/7**		**6/8**
	Pogonus transfuga	teneral					/4	8/10	/7	3/7	1/3									3/4			
		immature		/4	/1	/1	2/	10/12	10/6	7/2	4/	1/3	2/1	3/		/1		/1					
		mature P	147/99	104/98	25/29	18/29	7/6	2/												108/64	86/33	12/6	48/18
		mature A	/1	/1	/5	6/17	/7	5/12	7/9	2/2	2/3	3/3	1/2	9/6						128/91	64/63	11/12	24/23
		spent P		/3				/1	/2	/1				/1	1/	2/1	2/1	6/6	5/3	6/12	/2	/1	/2
		spent A	/1	/1									/1			/1							
		Total	**147/101**	**104/107**	**25/35**	**24/47**	**9/17**	**25/35**	**19/24**	**15/11**	**11/6**	**4/6**	**3/4**	**12/6**	**1/**	**2/2**	**2/1**	**6/6**	**5/3**	**245/171**	**150/101**	**23/19**	**72/44**
Reedbeds	*Pogonus transfuga*	teneral						2/4	2/3	4/5	1/3												
		immature	/1			1/1		3/9	/5	2/3	/1									9/18			
		mature P	22/30	16/29	19/16	5/1									1/					40/24	22/18	20/19	48/37
		mature A			5/1													2/	2/1		6/3	7/6	15/8
		spent P					1/1	1/	/2	/1	1/					1/			2/1	15/3			2/1
		spent A																		/4	/1	/1	/1
		Total	**22/31**	**16/29**	**10/16**	**5/1**	**2/1**	**6/13**	**2/10**	**6/9**	**2/4**			**1/**		**1/**		**2/1**	**8/8**	**64/49**	**28/22**	**27/26**	**63/49**

Notes. Numerator – number of males, Denominator – number of females; P – parental generation; A – ancestral generations

30-40 days. In *C. chloroticus*, *Pogonus transfuga*, *P. meridionalis*, *Pogonistes rufoaeneus*, *P. angustus* and *P. convexicollis*, the maximum spring activity was pronounced. During this maximum, at least 50% of total numbers of each species were observed (Table 1). The period of maximum activity varied strongly from species to species. In *P. transfuga* and *P. meridionalis*, it lasted about 60 days from early April until the end of May; in *P. rufoaeneus* and *P. convexicollis*, it lasted for a period of less than 30 days in May; in *C. chloroticus* it lasted for only 10 days during mid April.

During the period of maximum locomotor activity, mature beetles of all the above mentioned species were more abundant than immature ones. *Pogonus transfuga*, *P. meridionalis* and *Pogonistes rufoaeneus* were found to be iteroparous, because some specimens belonged to the ancestral generations, i.e. had already oviposited during the preceding years. In *P. meridionalis* and *P. rufoaeneus*, the proportion of spent beetles in each of the ten-day catches did not exceed 12%; in *P. transfuga* the proportion amounted to 25-33% in the reedbeds and to 52-58% in the salinas. In contrast, *C. chloroticus*, *P. angustus* and *P. convexicollis* were semelparous species, because their populations included only beetles of the parental and daughter generations (Table 1).

The maximum number of ripe eggs in the females of most of the studied species did not exceed 9; only in *P. transfuga* were 20 eggs found. The number of eggs per female averaged between 2.1-2.8, except for both *P. meridionalis* and *P. transfuga* 4.7 and 5.3 eggs, respectively, were recorded (Fig. 2). The dynamics of oviposition correlated well
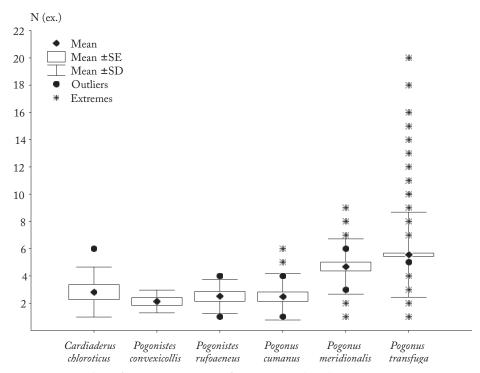

Fig. 2. Mean number of eggs in six species of Pogonini in the Elton region.

with seasonal activity in the habitats. In reedbeds, oviposition of *P. transfuga* occurred from mid May to early June in 2006 and from early to mid April in 2007, whereas in the salinas it occurred from mid May to mid June in 2006 and early April in 2007 (Fig. 3A-B). The average number of eggs per female was higher in the parental generation than in the ancestral generations. In the reedbeds, the differences were significant in some cases (Fig. 4A), whereas they were not significant in the salinas on the floodplain terrace (Fig. 4B). In reedbeds, sometimes the average number of eggs per female was significantly lower in the ancestral generations than in the parental generation (Fig. 4A). In contrast, in salina on a floodplain terrace, the average number of eggs per female of ancestral and parental generations was non-significant in all cases (Fig. 4B).

In *P. rufoaeneus* and *P. convexicollis*, the maxima of oviposition were recorded from early to mid May, in *P. meridionalis* from mid May to mid June in 2006 (Fig. 3C) and from mid April to early May in 2007.

The larval development in all these species was completed during one growing season. However, the duration of development strongly depended on the environment. The first larval instar of *P. transfuga* were observed from the beginning of May to early June. By mid May, some of them reached the third instar stage while the first pupae oc-
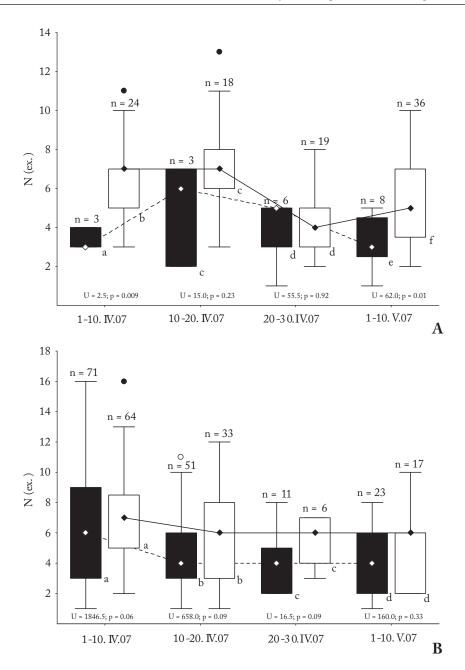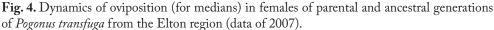

Fig. 3. Dynamics of oviposition (for means) in three species of *Pogonus* in the Elton region. A-B – *P. transfuga*; C – *P. meridionalis*; D – *P. cumanus*; boxes – means ± SE; whisker – means ± SD; dark grey boxes – reedbeds along the Khara River; open boxes – salinas on a floodplain terrace of the Khara River; light grey boxes – lakeside salt-marsh.

Fig. 4. Dynamics of oviposition (for medians) in females of parental and ancestral generations of *Pogonus transfuga* from the Elton region (data of 2007).

A – reedbeds along the Khara River; B – salina on a floodplain terrace of the Khara River; boxes – 25%-75%; whisker – non-outlier ranges; circles – outliers; open boxes – parental generation; filled boxes – ancestral generations; same letters indicating statistically non-significant differences; different letters indicating statistically significant differences (p<0.05; U-test).

curred from the end of May (Table 2). At the same time, in most of the species, females with ripe eggs could be found over a long period: in *P. convexicollis* up to mid June, in *P. transfuga*; to the end of June, in *P. meridionalis* until early July, and in *P. rufoaeneus* and *C. chloroticus* to the end of August. As a result, depending on the species, all instar larvae were encountered until mid August, or even up until early September. The duration of their development was considerably longer compared to the larvae which developed at the beginning of the growing season (Table 2).

The end of the reproduction period was characterized by an activity decline from the middle to the end of June. During this period, the proportion of spent beetles increased in the population while the first individuals from the new generation developed. A 1-1.5 month interval was found between the maximum reproduction and the appearance of the new generation. The new generation accounted for ¾ of the activity in the peaks of July-August. The peak of activity in September-November was more even. Immature adults from the daughter generation, as well as some beetles from the parental and ancestral generations, were mainly represented in this peak.

Variation in the life cycles was insignificant between the different habitats. For example, in *P. transfuga*, the activity of breeding beetles in the salina decreased more quickly than in the reedbeds (Table 1). In the salinas, the average number of eggs per female varied from 4.7 to 5.1 (2006) and 4.4 to 6.5 (2007). In the reedbeds it varied from 7.3-8.3 to 5.0 (2006) and 6.3-6.9 to 4.9 (2007)(Fig. 3A-B).

Hence, the life cycles of all these species are monovariant monovoltine with spring or spring-summer reproduction and adult (immature or both immature and spent) hibernation. However, the interpretation of the *C. chloroticus* life cycle is equivocal. This species is a spring-breeder. Under laboratory conditions, however, larvae reared from beetles that were transferred from the field to the laboratory in the beginning of June,

Table 2. Duration of pre-imaginal stages (in days) in several species of Pogonini in the Lake Elton region (data for 2006-2007, laboratory conditions).

Species		Time of development			
		Dates	Min-Max	Average duration of development (mean ± SD)	Median
Pogonus transfuga	L_1 (n = 6)	1-9.V.2007	6 - 9	7.0 ± 1.1	7.0*
	L_2 (n = 6)	7-17.V.2007	6 - 10	7.7 ± 1.5	8.0**
	L_3 (n = 5)	14-24.V.2007	7 - 11	8.6 ± 1.5	8.0***
Pogonistes rufoaeneus	L_1 (n = 2)	3-14.IX.2006		12.0 ± 0	12.0*
	L_3 (n = 1)	29.VII-14.VIII.2006		17.0	
Cardiaderus chloroticus	L_1 (n = 1)	28.VIII-3.IX.2006		7.0	
	L_2 (n = 4)	15.VIII-3.IX.2006	11 - 20	17.8 ± 4.5	20.0**
	L_3 (n = 3)	15.VIII-5.IX.2006	16 - 22	19.0 ± 3.0	19.0***

Notes: The medians with the same left symbols are compared with each other ($p<0.05$, U-test); * - U = 0; Z = -2.0; p = 0.045; ** - U = 0; Z = -2.56; p = 0.01; *** - U = 0; Z = -2.34; p = 0.025.

emerged in August. Under natural conditions, the last larvae of the third instar were found in October. Possibly, the life cycle of *C. chloroticus* is bivoltine, hence multivariant. The high activity of mature males from the end of July to early August supports this suggestion. The absence of females with ripe eggs from the catches was probably related to their low locomotor activity during the hot and dry second half of the summer.

In contrast, the maximum activity in *P. cumanus* was from the beginning of August to the end of September. Freshly emerged beetles from the new generation, as well as adults from the ancestral generations, were observed from mid May to early June. The proportion of the latter in the ten-day catches ranged from 100% to 67%. From mid-June to mid-July, no activity was recorded. The second peak of activity in non-breeding beetles from the new and ancestral generations was from the middle of July to mid of August. The share of the latter in the ten-day catches was reduced to 11%. The maximum reproduction occurred from the end of August to early September (Table 1).

The maximum number of ripe eggs amounted to 6, and the average per female was 2.5 (Fig. 2). The peak of oviposition was at the beginning of September (Fig. 3D).

Spent beetles and larvae from the *P. cumanus* population were found to enter hibernate from the end of September to the end of October.

Thus, *P. cumanus* is an iteroparous species with an autumnal breeding period. Its life cycle is monovariant monovoltine with obligatory larval hibernation and obligatory adult aestivation parapause.

Spatial and temporal pattern and dispersal potential

The spatial and temporal pattern of activity density was analyzed for seven Pogonini species with respect to their habitat. *P. transfuga* and *P. meridionalis* were more abundant in moderately to poorly salinated habitats. While *P. meridionalis* lived only on salinas on floodplain terraces, *P. transfuga* also inhabited reedbed thickets along river banks (Fig. 5). In the latter species, the peak of locomotor activity was observed 20 days earlier than that of the former species (Table 1).

All the other species were more abundant in habitats with high salinity (Table 1). *C. chloroticus*, *P. cumanus*, *P. rufoaeneus*, *P. angustus* and *P. convexicollis* inhabited only lakeside salt-marshes. *P. rufoaeneus* additionally inhabited floodplain salinas, as well using river banks as corridors (Fig. 5). Only *P. cumanus* was an "autumn" breeder (according to Larsson, 1939), while the others were "spring" breeders (Table 1). At least *C. chloroticus* preferred humid sites of salt-marshes with deep soil cavities. *Pogonistes* species inhabited different microhabitats, e.g. inside debris, under the salt crust, and in small soil crevices.

All studied specimens of the Pogonini were macropterous. However, their dispersal potential varied. More than 80% individuals of *C. chloroticus* and *P. rufoaeneus*, and more than 90 % specimens of *P. angustus* and *P. convexicollis*, had wing muscles. A decrease in *Ipm* value was observed during the period of maximum reproduction or at the end of the growing season. This decrease resulted from the activity of mature and spent beetles
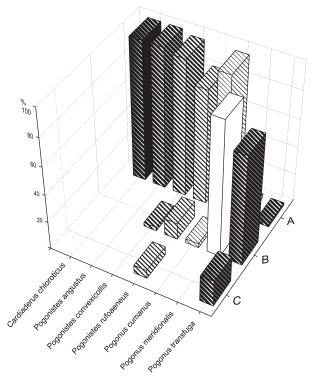
Fig. 5. Spatial distribution of seven species of Pogonini in the Elton region.
A – lakeside salt-marsh; B – salina on a floodplain terrace of the Khara River; C – reedbeds along the Khara River.

of the parental generation. In contrast, adults with fully developed wing muscles in the three *Pogonus* species were less abundant. The value of *Ipm* amounted to 0.5, 0.6 and between 0.32 and 0.86 in *P. cumanus*, *P. meridionalis* and in *P. transfuga*, respectively. In the latter two species, the maximum value of *Ipm* was recorded in May or in June-July, during the emergence of young beetles (Table 3).

Infestation by parasites

During our study, parasitic mites of the family Podapolipidae were reported for the first time on *P. transfuga*, *P. meridionalis*, *P. cumanus* and *P. rufoaeneus*. In some species, for example *P. transfuga*, 16% of the specimens were infested. In April and May, only beetles of the ancestral generations were infested, whereas in July-October specimens of the parental generation were infested (Table 4). Mites were invariably located ventrally at the base of the wings which is considered to be their typical location on their hosts (Regenfuss, 1972). Each wing carried one female and groups of eggs and nymphs. Asymmetric arrangements of mites were recorded in only a few cases.

Table 3. Seasonal changes in *Ipm* values in Pogonini species from different habitats in the Lake Elton region (pooled data for 2006-2007).

Habitats	Species	Sex	Months						
			IV	**V**	**VI**	**VII**	**VIII**	**IX**	**X**
Lakeside salt-marsh	*Cardiaderus chloroticus*	♂	0.62	1.0	1.0	1.0	1.0	1.0	1.0
		♀	0.71	1.0	1.0	1.0	1.0	1.0	1.0
	Pogonistes angustus	♂			1.0	1.0		1.0	
		♀			1.0	1.0	0.5	0	1.0
	Pogonistes rufoaeneus	♂	0.75	0.95	1.0		0.55	1.0	
		♀	0.7	1.0	0.67	0.6	0.17	1.0	1.0
	Pogonistes convexicollis	♂	1.0	1.0	1.0	1.0	0	0	1.0
		♀	1.0	1.0	1.0	1.0	0	0	1.0
	Pogonus cumanus	♂			0	1.0	0.33	0.39	0.5
		♀	0		0	1.0	0.29	0.29	0
Salina on a floodplain terrace	*Pogonus meridionalis*	♂	0	0.35	0.36	0	0.6	1.0	
		♀	0	0.2	0.15	0	1.0		
	Pogonus transfuga	♂	0.02	0.32	0.19	0.02	0.11	0.07	0.15
		♀	0.03	0.26	0	0	0.13	0	0.1
Reedbeds	*Pogonus transfuga*	♂	0.16	0.24	0.71	0.86	0.5	0	0.21
		♀	0.09	0.32	0.33	0.8	0.75		0.21

Table 4. Seasonal changes in infestation rates (in %) *Pogonus transfuga* by Podapolipidae mites in the Lake Elton region (pooled data for 2006-2007).

Habitats	Sex	Months						
		IV	**V**	**VI**	**VII**	**VIII**	**IX**	**X**
Salina on a floodplain terrace	♂ P							33.3
	♀ P				80.2			75.4
	♂ A	53.5	78.5					
	♀ A	40.0	33.3					
Reedbeds	♂ P				72.7	70.0	72.7	63.6
	♀ P				96.1	87.5	85.7	88.8
	♂ A	50.2	70.8					
	♀ A	63.3	76.0					

Notes. P - parental generation; A - ancestral generations.

DISCUSSION

Contradictory observations have been published concerning the life cycles of Pogonini. Turin (2000) found a spring-summer type of seasonal activity in *Pogonus chalceus*, *P. litoralis* and *P. luridipennis*. However Larsson (1939), Heydemann (1962) and Paarmann (1976) considered *P. chalceus* to be a summer breeder. In the Elton region, the maximum reproduction activity in most of the Pogonini species is confined to April to May. This is probably affected by air temperatures and relatively high soil moisture rates during a short spring. Similar observations are available for salt-marshes in Belgium, where the maximal reproduction activity of *P. chalceus* was also recorded in May (Desender, 1985, 2000). Differences in egg-production between old and young females have been reported for *Calathus melanocephalus* (van Dijk, 1979), several *Carabus* spp. (Grüm, 1975) and *Pterostuchus melanarius* (Matalin, 2006). In these species, the average number of eggs in old females was lower than that in young individuals.

Detailed information concerning the duration of pre-imaginal stages is known only for *P. litoralis*. Under laboratory conditions, the larvae developed in 22-24 days and pupae in 15-17 days. Total development from egg to imago lasted 42-48 days (Nekuliseanu, 1987). Such results correspond well with our data on the development of a related species, *P. transfuga* (Table 2).

Gonad maturation has been studied only for *P. chalceus* and *P. litoralis*. Gonad maturation in *P. chalceus* is induced by high air temperatures in northern Africa, with reproduction observed during the summer months. Under such conditions, two generations are produced (Paarmann, 1976). However, in Northern Europe the life cycle of *P. chalceus* is monovoltine (Larsson, 1939; Paarmann, 1979; Desender, 1989; Turin, 2000). A similar life-cycle is known for several species of *Stenolophus* (Matalin, 1997c). In contrast, gonad maturation in *P. litoralis* is completed only after hibernation (Neculisaenu, 1987).

According to our data as well as those of Larsson (1939), six species of Pogonini are "spring" breeders. Already in the first half of April, nearly 90% of specimens of *P. transfuga*, *P. meridionalis* and *C. chloroticus*, as well as 50% of specimens of *P. rufoaeneus* and *P. convexicollis*, can reproduce (Table 1). In these species, maturation of gonads follows the Type 1 pattern described by Thiele (1977). Only *P. cumanus* is an "autumn" breeder. This is surprising, because hitherto all Pogonini have been considered as "spring" breeders or "imaginal" hibernators (Larsson, 1939; Heydemann, 1962; Paarmann, 1976, 1979; Desender, 1985, 1989, 2000; Lindroth, 1992; Turin, 2000; Matalin & Makarov, 2006). Although the new generation of *P. cumanus* emerges in mid May to early June, they reproduce from the end of August to the end of September. Thus, gonad maturation corresponds to the Type 4 pattern described by Thiele (1977).

Like most carabid beetles, all of the studied species of Pogonini are opportunistic predators. As they are similarly sized, we presume that they compete for food. Moreover, six species show the same type of life-cycle and, hence, are potential competitors for living space. To reduce competition, they must partition their habitat in space and/or in time

(Andersen, 1983, 1988; Matalin, 1997a; Brandmayr & Algieri, 2000). This is attained by varying habitat preferences and different life cycle strategies.

Among the studied species, *P. transfuga* and *P. meridionalis* can be regarded as halophiles, because they live in habitats with moderate salinity. To diminish competition, heterogeneous within- and between-habitat distributions (Fig. 5), heterochronous maxima of locomotor activity (Table 1), as well as size differences (*P. transfuga* is larger than *P. meridionalis*) are applied. The other five species are halobiontic because, with only a few exceptions, they occur only in habitats with high salinity (Fig. 5). Among them, only *P. cumanus* is an "autumn-breeder", while the others are "spring-breeders (Table 1). *C. chloroticus* seems to be a more specialized beetle, because it inhabits highly specific microhabitats and possibly has a bivoltine life-cycle. Competition in the three *Pogonistes* species seems to be higher, as they are similar in size and inhabit the same, or similar, habitats. Only *P. rufoaeneus*, the most abundant species, inhabits all of the studied habitats, while *P. angustus* and *P. cinvexicollis* are less abundant and coexist with *P. rufoaeneus* in salt-marshes only.

The discovery of Podapolipidae mites on Pogonini beetles is remarkable. Until now, only species from the tribes Carabini (Eidelberg, 1994; Fain et al., 1995; Regenfuss, 1968), Scaritini (Husband, 2001), Broscini (Eidelberg, 1994), Bembidiini (Eidelberg & Husband, 1993), Platynini (Eidelberg, 1994; Fain et al., 1995; Husband, 1998), Pterostichini (Eidelberg, 1994; Husband, 1998c; Husband & Dastych, 2000), Zabrini (Eidelberg, 1994; Husband & Husband, 1996), Harpalini (Husband, 1998a, b), Panagaeini (Husband, 2000), Callistini (Eidelberg, 1994; Husband & Dastych, 1998), Lebiini (Fain et al., 1995) and Trichognathini (Husband & Eidelberg, 1996) have been known as hosts of Podapolipidae.

The biology of Podapolipidae is still poorly known. These mites are known to show complicated life-histories and to be ectoparasites of different insects (Husband, 2000, Regenfuss, 1968). High specialization is typical of Podapolipidae, because they are usually associated with only one or two host species (Fain et al., 1995; Regenfuss, 1968). Beetles usually become infested during copulation with an infested mate. Apparently, this sharply restricts the mites' dispersal capacity (Regenfuss, 1968) and corresponds well with our observations. Mites have only been found on beetles in copula. Since numerous Carabidae species are known to reveal high mortality rates during hibernation as imago, the capability of some spent beetles to survive winter and to reproduce in the next year together with specimens of the new generation are, we suggest, important preconditions for the successful development of Podapolipidae. On the other hand, this greatly restricts the range of their potential hosts. In September-October, the proportion of already copulated and infested specimens of *P. transfuga* was about 70%, whereas it was 58.5-55.5% during April to May (Table 4).

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