Ethology and ecology of *Merodon* in Turkey (Diptera: Syrphidae)

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Abstract: Behavioural and ecological elements in the biology of five species of *Merodon* Meigen were studied in Turkey. *M. aberrans* Egger, *M. avidus* Rossi, *M. loewi* Van der Goot and *M. telmateia* Hurkmans defended territories. *M. planiceps* Loew possibly showed latent territoral behaviour. Males of *aberrans, loewi* and *telmateia* defended territories by approaching intruders and buzzing, *avidus* males chased intruders. In *aberrans, loewi* and *telmateia* defense may be partly triggered by sound. *M. aberrans* and *telmateia* occupied the wettest habitats available; *M. loewi* might have this preference as well. *M. loewi* females showed behaviour toward *Gladiolus* plants. Some *Merodon* species seemed to prefer rather wet biotopes in general.

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Introduction

Apart from the extensive literature on the economically important narcissus bulb fly *Merodon equestris* Fabricius, which concentrates mainly on the life cycle and economical damage, little information is available on *Merodon* behaviour and ecology. There have been studies by Conn (1976, 1978) and Fitzpatrick & Wellington (1983) on *M. equestris*, and by Hurkmans (1985) on *M. clavipes* Fabricius and *M. pruni* Rossi. These dealt with male territorial behaviour (Fitzpatrick & Wellington, Hurkmans) and population size estimation and influence of morphology on behaviour (Conn.). The present paper is a preliminary study into the ecology and behaviour of five other *Merodon* species, viz. *M. aberrans* Egger, *M. avidus* Rossi, *M. loewi* Van der Goot, *M. planiceps* Loew and *M. telmateia* Hurkmans. This paper does not supply the reader with definite answers but hopes to stimulate further research into this interesting genus.

Localities

The species mentioned were studied at four different localities in Turkey. These localities were (see fig. 1): (1) N. of Başkale, Mengene Dağı, Van district, 2700-3000 m, Turkey, visited June 26-28, 1986; (2) 5 km. E of Sarıkamış, Kars deresı valley, Kars district, 2000 m, visited June 30-July 5, 1986; (3) Hamsiköy, Zigana Dağı, Trabzon district, 1600 m, visited July 8-12, 1986; (4) Tamdere, Giresun Dağı, Giresun district, 1700 m, visited July 14-17, 1986. Tables 1 and 2 present some additional data on the localities. The Kars deresı valley proved best for study of *Merodon* behaviour. A map showing various biotopes at this locality is given in fig. 2.

Methods

Observations began between 8.00 and 9.00 h and were continued until about 15.30 h. Individual specimens were marked on the thorax with dilute typewriter correcting fluid in order to distinguish them. The duration of behavioural elements at locality 2 was measured by means of a stopwatch. At this locality "buzzing" experiments were done to obtain information on reaction by *Merodon* males to auditory stimuli. The buzzing was produced by blowing on a reed firmly held between the thumbs, or blowing through the fingers pressed together. In order to study reaction to

Fig. 1. Situation of the localities in Eastern Turkey.

visual stimulus, mechanically killed flies (this to prevent odour) were tied to a thin dark thread and moved up and down in front of male *Merodon* specimens at various distances between 10 and 50 centimetres. To test the attachment of males to the territory they occupied, individual males were captured more than once, while the time needed to return was recorded. Marking and subsequent release of males was done at the capture spot at all localities.

Observations

At localities 1, 3 and 4 no true territorial behaviour was observed. At locality 1 four *M. avidus* males were marked, but did not return. Several other *M. avidus* males were seen but they were very easily disturbed and could not be captured. They flew at 20-30 cm above ground level through the vegetation. No confrontations were seen, and no females were found here.

At locality 3 *M. planiceps* males flew very close to ground level through the short vegetation. Six males caught and marked did not return. Confrontations between *planiceps* males were observed, the males inspecting one another at close range. They did not make physical contact, and the confrontations lasted very shortly. No female *planiceps* were recorded here.

Table 1. Conditions at four localities.

Locality	Biotope	Vegetation	Weather
1 (Başkale)	Grassland on hillsides and valley bottom in area without woods	Many Scrophulariaceae, Orchidaceae and Labiatae	Temperature -2 to + 26 °C, sunny, slight winds
2 (Sarıkamış)	Moderately wet to very wet grasland and marsh in wooded valley	Many Orchidaceae, Compositae, Umbelliferae and Liliaceae	Temperature + 14 to + 31 °C, sunny, wind Beaufort 2 to 3
3 (Hamsiköy)	Mown grassland in steep open valley with scattered woods	Many Ranunculaceae, Compositae and Orchidaceae	Temperature + 12 to + 24 °C, overcast, slight winds
4 (Tamdere)	Exposed mountainside with grassland alternating with patches of wood and shrubs	Many Compositae, Labiatae, Orchidaceae and Liliaceae	Temperature + 10 to + 20 °C, overcast, slight winds

At locality 4 eight *planiceps* males were marked, but did not return. The males were patrolling flight paths along the contour of the slope (14 observations) but were hardly seen flying up and down the slope (1 obs.). When *planiceps* males met one another (6 obs.), they inspected and in some cases chased one another (4 obs.). The female *planiceps* flew close to the ground through the vegetation, with no obvious preference for any orientation to the slope direction. The observed *Merodon* specimens at localities 1, 3 and 4 generally flew close to the ground level and could not be recaptured after marking, so that their abundance could not be estimated.

At locality 2 territorial behaviour of four species, viz. *M. aberrans, M. avidus, M. loewi* and *M. telmateia* was observed; the territories occupied by the males of the respective species are shown in fig. 3. Especially *telmateia* was present in large numbers, but *avidus, aberrans* and *loewi* also were abundant. Only *loewi* females were less frequent; about ten specimens were observed.

The *aberrans* males occupied the wettest habitats; all seven territories observed were found in marsh vegetation strips, that were however not fully occupied by *aberrans* males. The territories of *aberrans* were estimated to be 3 to 8 m^2 large and included suitable food plants for the adult flies, like various Umbelliferae, *Ornithogalum* sp. and *Gladiolus* sp. These territories seemed to be centred on relatively high growing *Carex* plants and white flowering Umbelliferous plants. The *aberrans* males behaved aggressively toward intruders of about their own size, mostly *aberrans* and *avidus* males (20 obs.). They defended by flying at the intruder, landing close and buzzing loudly. This buzzing sound was audible at several metres' distance. In three cases the intruder was briefly chased but physical contact was not observed. If undisturbed the *aberrans* males sat in the centre of the territory. The female *aberrans* flew very close to ground level. They were usually left alone by the *aberrans* males, but sometimes expelled (2 obs.). Copulation was observed twice, the male being on top of, and slightly behind the female. The copulations took place on inflorescences in the centre of territories. After copulation the males maintained their territory.

The *avidus* males seemed to have a less specific preference for any habitat found at locality 2. Nine territories mapped were found in the marsh strips, the drier grassland and also on the slopes and top of the railroad embankment. These territories ranged from 4 to 12 m^2, included generally the same food plants as in the *aberrans* territories, but on the embankment also included several yellow flowering Umbelliferae. Most of these territories were centred on yellow flowering Umbelliferous plants of various sizes.

The *avidus* males behaved aggressively toward insects of roughly their own size, mostly *aberrans* and *avidus* males (over 25 obs.). They defended by chasing (over 25 obs.), sometimes followed by physical contact (2 obs.). In one case, an *avidus* territory was not reoccupied after an intrusion followed by chasing. If undisturbed the *avidus* males sat in the centre of their territories. The *avidus* females flew at 40-60 cm above ground level, and were often seen on inflorescences. Twice they were expelled

Table 2. Presence of species at four localities.

Locality	*avidus*	*aberrans*	*loewi*	*planiceps*	*telmateia*
1 (Başkale)	♂♂	–	–	–	–
2 (Sarıkamış)	♀♀, ♂♂	♀♀, ♂♂	♀♀, ♂♂	–	♀♀, ♂♂
3 (Hamisköy)	–	–	–	♂♂	–
4 (Tamdere)	–	–	–	♀♀, ♂♂	–

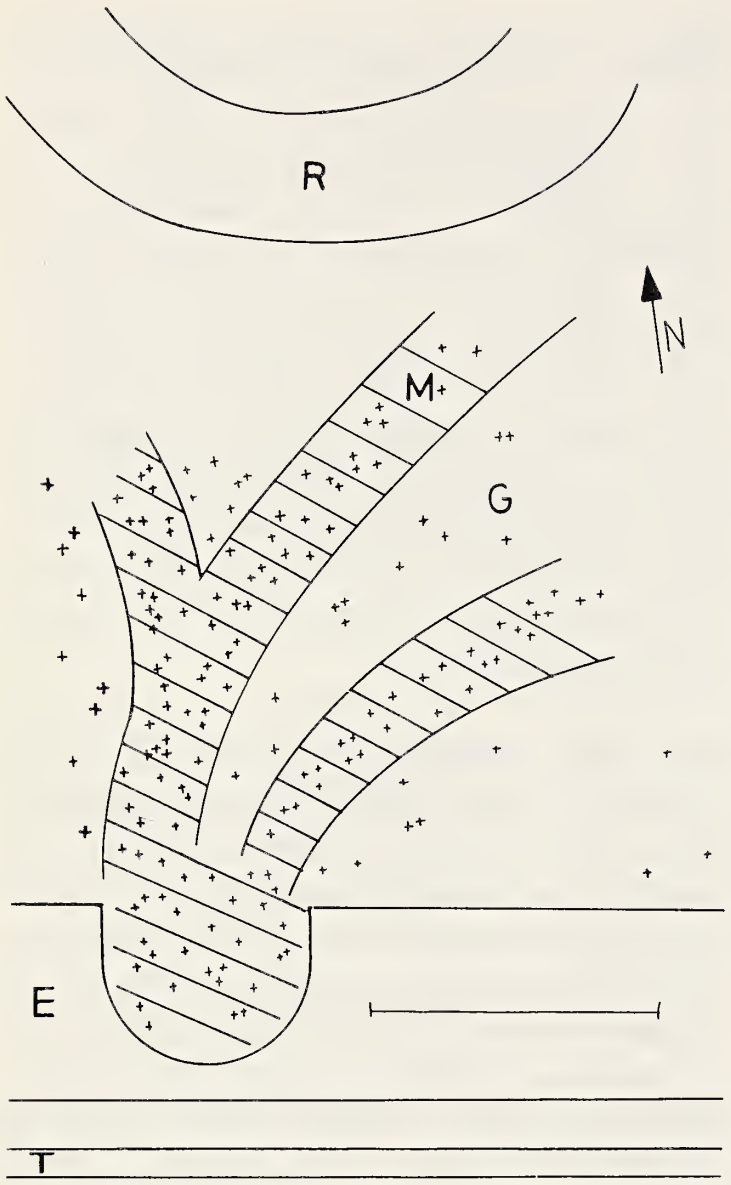

Fig. 2. Map of locality 2 (Sarıkamış) showing vegetational units. R = Kars deresi rivulet; M = strips of marsh vegetation; G = grassland; E = railway embankment; T = railway track; + = flowering *Ornithogalum* plant (Scale line 10 m).

from territories occupied by *avidus* males.

The *loewi* males occupied territories adjacent to the strips of marsh vegetation in the grassland habitat. Eight territories with an estimated size of 3-8 m^2 were found in the study area. These included generally the same food plants as the *aberrans* territories, and were centred on inflorescences of *Ornithogalum* sp. Defense was by approaching intruders, followed by loudly buzzing (over 20 obs.), patrolling the territory borders (2 obs.), or chasing (2 obs.). The *loewi* males did not make physical contact with intruders. They tried to expel intruders of their own size mainly, but also harrassed intruding *aberrans* and *avidus* males (these confrontations were relatively seldom and not vigorous). When sitting on the ground or on leaves, they sometimes produced a shorty buzz repeated at intervals of some 10 seconds (4 obs.). When not engaged in territorial defense they sat in the centre of the territory, usually on inflorescences of *Ornithogalum* sp. The females flew at 30 cm above ground level or lower. When approached by the *loewi* males they were not seen to be expelled. These females were seen to sit on *Gladiolus* sp. stems, some 3 cm above ground level, pressing their abdominal apex to the plants (8 obs.). This procedure lasted from 32-63 seconds and was, during this time, interrupted 5-7 times. As this might have been oviposition the stems were thereafter checked for little holes, but none were found. Some stems were dug out and preserved, but no larvae or adult flies could be reared.

The *telmateia* males seemed to prefer the wettest habitat present in the study area. Over 20 territories, only about 1-2 m^2 in surface were found. These were centred on inflorescences of

Table 3. Number, habitat, size and overlap in *Merodon* male territories at locality 2 (Sarıkamış).

Species	Number of territories studied	Habitat	Estimated size	Overlap with *aberrans*	Overlap with *avidus*	Overlap with *loewi*	Overlap with *telmateia*
aberrans	7	Marsh	3- 8 m^2	–	no	no	13 cases
avidus	9	no clear preference	4-12 m^2	no	–	no	6 cases
loewi	8	Grassland adjacent to marsh	3- 8 m^2	no	no	–	no
telmateia	27	Mainly marsh	1- 2 m^2	13 cases	6 cases	no	–

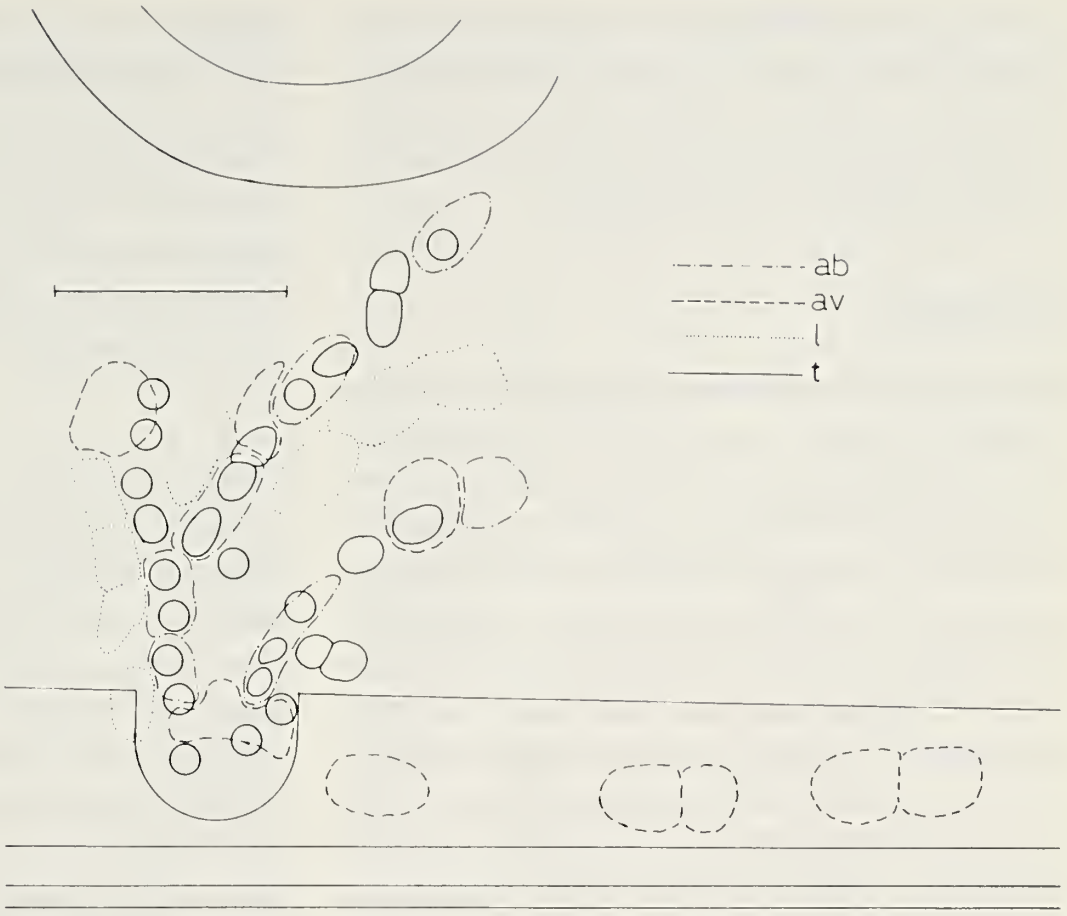

Fig. 3. Map of locality 2 (Sarıkamıs) showing territories studied with their boundary in the observation period. ab: *aberrans*; av: *avidus*; l: *loewi*; t: *termateia* (Scale line 10 m).

Ornithogalum sp. and in many cases overlapped partly or entirely with *aberrans* or *avidus* territories. Defense of the territory by *telmateia* males was rather lukewarm, mostly only by approach and inspection (over 30 obs.), sometimes by sitting close and buzzing (7 obs.). The buzzing sound emitted by the *telmateia* males was much higher than that of the *loewi* and *aberrans* males. Defense was only directed at conspecific males, as far as observed. In some cases, after an intrusion the territory was inspected all over (4 obs.) after which the occupant returned to the centre. The female *telmateia* were never expelled or confronted with buzzing. They flew at about 10 cm above ground level and spent much of their time on *Ornithogalum* inflorescences, even when already occupied by *telmateia* males.

At all four localities the males were active already at the start of observations, at air temperatures as low as 14 °C (ground temperatures usually were higher than air temperatures but could not be measured). Reduced activity during the mid-day period was not found.

Experiments

Territories of various *Merodon* species were seen to overlap one another. Still, defense can be quite aggressive in several species. To ascertain if the occupying males reacted to visual stimuli in absence of other stimuli, dead conspecific specimens were trailed past occupying males, or moved up and down in front of them. This provoked approach, and after that a quick loss of interest in *avidus*, and no reaction at all in the other species. To test the reaction to auditory stimuli in absence of visual stimuli, a buzzing sound was produced. This yielded no reaction in *avidus* males, but males of *aberrans, loewi* and *telmateia* all reacted by inspecting the territory from the lookout-post in the centre, or actually patrolling (in *loewi*) part of the territory (5, 6, 7 obs. respectively). The buzzing test produced best results when the sound was of about the same pitch as that produced by the tested species. This pitch was highest in *telmateia*, lowest in *aberrans* and intermediate in *loewi*, and therefore might be related to size (*aberrans* averages some 13 mm body length, *loewi* 10 mm and *telmateia* 7), in the same way wingbeat sound is.

To test the attachment of males to their

territory, males already marked were captured again and released. This was tried at locality 2 with four *aberrans* males and five *avidus* males. All these returned to their territory in times ranging from 3-20 minutes.

Discussion

At locality 2 mutual exclusion of *aberrans* and *avidus* territories was found. These territories also excluded *loewi* territories. The *loewi* and *telmateia* territories were mutually exclusive as well, but *tematei*a territories were found to overlap with *aberrans* and *avidus* territories. The larger *aberrans* and *avidus* (about 14 mm body length) tolerated the much smaller *termateia* but diligently expelled insects of their own size. In view of the results of the buzzing experiments it might be possible that territorial defense in *aberrans*, *loewi* and *telmateia* is partly triggered by sound. In particular, sound corresponding to the sound emitted by the defender produced strong reactions in the experiment. As the pitch of the sound is probably related to insect size (it is produced by the wings) this might explain why the larger species leave the smallest one alone, and all try to expel the intermediate *loewi*, except for *telmateia* which reacts only to its own species. The "adjustment" of reacting only to more or less specific frequencies is economical in terms of effort spent in defense, as no energy is "wasted" on relatively harmless intruders.

Severinghaus et al. (1981) describe that in the bee *Anthidium* "patrolling males also chased many other species of insects... these insect ranged from tiny halictid bees to carpenter bees (*Xylocopa*) larger than the males themselves" and also that "male *A. manicatum* actually defend their territories more frequently against other species of insects than they do against other *Anthidium* males... the aggressive, sometimes crippling behaviour directed against interspecific intruders is more violent than that toward conspecifics". The behaviour of the male *Anthidium* thus seems to imply a great waste of effort although indirectly the defenders may profit. In contrast the defense modes in *Merodon* as observed by Fitzpatrick & Wellington (1983), Hurkmans (1985) and as described in this paper, seem to be more economical. When conditions are crowded however, the *Merodon* males become much more aggressive toward all sorts of insects, as described by Fitzpatrick & Wellington (1983) and Hurkmans (1985), but even then they mainly attack insects of roughly their own size.

The phenomenon of sneaking by males who do not succeed in establishing their own territory has not been observed in the *Merodon* species discussed in this paper, nor has it been recorded in any other *Merodon*. This behaviour is described e.g. by Severinghaus et al. (1981) for the bee *Anthidium*, by Alcock et al. (1978) for several aculeate Hymenoptera, and by Tsabuki & Ono (1986) for the dragonfly *Nannophya*. Whereas Alcock et al. (1978) find that the sneaking males slip into the territories, repeatedly fleeing from the occupants' approaches and then re-entering the area until finally ignored, for several hymenopterous species, the reverse seems to be the case in *Merodon*. Fitzpatrick & Wellington (1983) and Hurkmans (1985) found that if intrusions into *Merodon* territories are frequent, defense becomes more fierce; probably the sneaking strategy does not pay under these circumstances. Alternatively, the size of the territory may be important, since relatively small territories can be well guarded even under crowded conditions.

The expelling of conspecific females by occupying males may be due to triggering of defense by auditory stimuli as suggested above, probably in absence of other (sexual, visual?) stimuli inhibiting defense. As not all females are expelled there must be an interplay of several types of stimuli, as noted e.g. by Alcock et al. (1978).

In some species of *Merodon* the defense of territories was discontinued under unfavourable conditions, e.g. high temperatures or overcast weather, as described by Fitzpatrick & Wellington (1983) and Hurkmans (1985). On

the other hand, some insects carry on defense in less favourable conditions as found by Tsabuki & Ono (1986) and described in this paper with respect to the hot mid-day period. Overcast weather was encountered at localities 3 and 4, where no territorial behaviour was seen. The behaviour of the *planiceps* males at locality 4 might be a precursor to territorial activity.

Several areas within the study terrain remained unoccupied by any *Merodon* males although female *Merodon* could be captured there along with males "passing by". The unoccupied parts of the study areas did not show conspicious differences from the occupied parts. If Alcock et al. (1978) are correct in assuming that territory probably is a function of male size and the number of male conspecific neighbours, which seems reasonable, this would imply that population density was low at locality 2 in all four studied species, since eligible sites remained unoccupied. In view of this it must be noted that under crowded circumstances the territorial defense by especially *aberrans*, *loewi* and *telmateia* might be very different from the modes now observed. Table 3 shows the number, estimated size and mutual overlaps of the territories found at locality 2.

The *loewi* males occupied territories adjacent, but outside the marshy strips. Since the *loewi* males were expelled from these strips by the occupying *aberrans* and *avidus* males it is possible that they really prefer the wetter habitat but are kept from occupying it, and then choose a "second best". The preference of *loewi* for the wetter habitats is likely since all territories were centred on *Ornithogalum* plants, which were much more frequent within the marshy strips than outside them. To establish the true preference in the *loewi* males more data are required.

At locality 2, males of *aberrans* and *avidus* were tested for their attachment to the territory they occupied. The males tested returned quickly. Conn (1976) found that males of *M. equestris* dispersed up to 100 m distance after capture and marking, but returned within 20-30 minutes. For *Eristalis tenax* (Linnaeus) Wellington & Fitzpatrick (1981) found that this hoverfly usually does not return after capture, marking and release. This species is less strongly territorial than most *Merodon* species, being more attached to sunny spots in the lee of the wind in general than to specific sites. Alcock et al. (1978) found that male site tenacity must be a function of the value of the area (and, probably, the chances of acquiring a new one). It seems that the characteristics of the insect are important, with respect to the stage of development the insect is in. If females abound there is likely to be more profit from occupying a territory, and therefore male site tenacity will probably be higher. The female behaviour may be of influence. Also the weather has been shown to be of importance. At localities 2 and 4, where female *Merodon* were present, the males (at least) confronted one another regularly. This indeed indicates that female presence might stimulate territorial behaviour or at least inter-male confrontations.

The difference in the defense modes used by the *avidus* males on one hand and the *aberrans*, *loewi* and *telmateia* males on the other, at locality 2, being more aggressive in the former, less so in the latter group, cannot be explained by any factor discussed above. Therefore this difference is preliminarly regarded as intrinsic.

Habitats occupied by *Merodon*

The localities where *Merodon* specimens were present during the field trip to Turkey in 1986 seemed to be the relatively wettest sites in their surroundings. At locality 1 at general conditions were dry, the locality itself being a wet strip along a mountain stream. Localities 2, 3 and 4 were in green, lush landscape, also in river valleys (2 and 3) or in open patches within large forests on hillside. Sack (1931) noted that the genus *Merodon* in general has its main distribution on the steppes of the Palaearctic region. It seems however, that a number of species occupy habitats in considerably wetter areas. Also a number of species are mountain dwellers which can be found up to 3000 metres altitude in alpine conditions. With respect to distribution over habitats the larval host plants

probably are more important than the general climate, as these probably can occur in small wetter enclaves in drier regions. Many species of *Merodon* occurring in dry areas complete their life cycles in the spring (in Europe and the Mediterranean region), thus avoiding the extreme summer drought. These species should therefore not be considered as xerophilic. This point of view is supported by several authors, e.g. van der Goot (1966) who recorded *Merodon* species on the slopes of Mount Etna in Sicily in high altitudes, and Marcos García (1984) who found *Merodon* species at various hillside and mountain localities in Spain. Also many specimens in the Rijksmuseum van Natuurlijke Historie (Leiden), the British Museum (Natural History) in London, the J. A. W. Lucas collection at Rotterdam and the collection of the Instituut voor Taxonomische Zoologie at Amsterdam, collected in high altitudes, confirm this. The extreme altitude of capture for a *Merodon* known so far is 3800 m, for a specimen of *M. turkestanicus* Paramonov from Iran, in the J. A. W. Lucas collection.

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