

Male territorial behaviour of the endemic large carpenter bee, *Xylocopa* (*Koptortosoma*) *ogasawarensis* (Hymenoptera: Apidae), on the oceanic Ogasawara Islands

SHINJI SUGIURA

Department of Forest Entomology, Forestry and Forest Products Research Institute (FFPRI), 1 Matsunosato, Tsukuba, Ibaraki 305-8687, Japan; e-mail: ssugiura@ffpri.affrc.go.jp

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Abstract. The endemic large carpenter bee, *Xylocopa* (*Koptortosoma*) *ogasawarensis* Matsumura (Hymenoptera: Apidae), on the oceanic Ogasawara (Bonin) Islands, located in the northwestern Pacific Ocean, approximately 1000 km south of the Japanese mainland, is a generalist flower visitor. Although the flower-visiting behaviour of *X. ogasawarensis* females has been frequently recorded, the behaviour of the males in this species has rarely been studied. I observed the territorial behaviour of males on flowers of the native plant species *Scaevola sericea* Vahl (Campanulales: Goodeniaceae) in a coastal area of Hahajima in early July 2007. Each male chose a particular inflorescence, hovered near it (mean distance, 239 mm from the inflorescence) and patrolled around it for several minutes (mean time, 331 s). Therefore, *X. ogasawarensis* males exhibit resource-based (i.e., flowers) territoriality. Males frequently attacked other males when defending their territories. However, males did not defend their territories against flower visitors of other species (i.e., introduced honeybees). Therefore, male territorial behaviour in *X. ogasawarensis* may be related to intra-sexual competition for sites visited by females. This is the first report describing the male territorial behaviour of *X. ogasawarensis*.

INTRODUCTION

Mating and territorial behaviour of males is reported for many bee species (Alcock et al., 1978; Eickwort & Ginsberg, 1980; Ayasse et al., 2001; Paxton, 2005). The sites where this behaviour occurs differ among bee species, e.g., nesting sites, emergence sites, overwintering sites, or food-plant flowers (Alcock et al., 1978; Ayasse et al., 2001; Sugiura et al., 2007). Large carpenter bees of the genus *Xylocopa* Latreille (Hymenoptera: Apidae) are interesting because the mating and territorial behaviour of male bees is very variable in this group (Gerling et al., 1989; Leys, 2000; Leys et al., 2000). The genus *Xylocopa* contains 469 species of moderately large to very large bees that are distributed over all continents, predominantly in tropical and sub-tropical climates (Michener, 2000). The genus *Xylocopa* consists of 31–51 subgenera, depending on the classification (Leys et al., 2002). *Xylocopa* males basically have three different ways of searching for females (Gerling et al., 1989; Leys, 2000): (1) searching at nesting sites, flowers, or landmarks (nonterritoriality); (2) monopolizing resources important to females, like flowers or nesting sites (resource-based territoriality); and (3) monopolizing areas lacking resources for females (nonresource-based territories, or leks). Although different types of mate-searching behaviour are reported for males, even within the same species of *Xylocopa*, some phylogenetic patterns in the mate-searching behaviour of *Xylocopa* males have been suggested (Leys, 2000). For example, nonresource territoriality seems to be characteristic for species in the subgenera *Neoxylocopa* Hurd & Moure and *Koptortosoma* Gribodo. However, further data on mating and territorial behaviour of *Xylocopa* (sensu lato) are needed in order to generalize these phylogenetic patterns.

The genus *Xylocopa* includes a few important endemic species on isolated oceanic islands that have never been connected to a continental landmass. Unique biotas are found on such

islands because of the separate evolution and speciation of immigrant organisms (Carlquist, 1974; Gillespie & Roderick, 2002). Because isolated oceanic islands originally lacked social bees, endemic solitary bees are considered to be important pollinators of oceanic island plants (Kato, 1992; Kato & Nagamasu, 1995; Olesen et al., 2002; Daly & Magnacca, 2003; Dupont et al., 2003; Abe, 2006; Philipp et al., 2006). *Xylocopa* (*Neoxylocopa*) *darwini* Cockerell, which is the only native (and endemic) bee species on the oceanic Galápagos islands, is known to visit the flowers of 79 plant species and is considered an important pollinator on these islands (Linsley et al., 1966; McMullen, 1993; Philipp et al., 2006). *Xylocopa* (*Koptortosoma*) *ogasawarensis* Matsumura, one of nine endemic solitary bees on the oceanic Ogasawara (Bonin) Islands (Kato, 1992; Kato et al., 1999), is also a generalist flower visitor and is considered an important pollinator of the plants on these islands (Goubara, 2002; Abe, 2006). On isolated oceanic islands, ecological release due to enemy- or competitor-free conditions is known to have induced endemic organisms to change their behaviour and habitats (e.g., Carlquist, 1974). Therefore, to generalize, the phylogenetic patterns in male territorial behaviour within the genus *Xylocopa* (sensu lato) make it particularly interesting for an investigation of the male behaviour of endemic island species. Males of *X. darwini* are recorded as defending shrubs or dead wood, but not flowers or nesting sites, i.e., they show nonresource territoriality (Linsley, 1965). However, male territorial behaviour in *X. ogasawarensis* is not described in detail. Here the territorial behaviour of male *X. ogasawarensis* in which male bees defend territories around the flowers of a native plant species against other males is reported. This is the first report describing the male territorial behaviour of *X. ogasawarensis*.

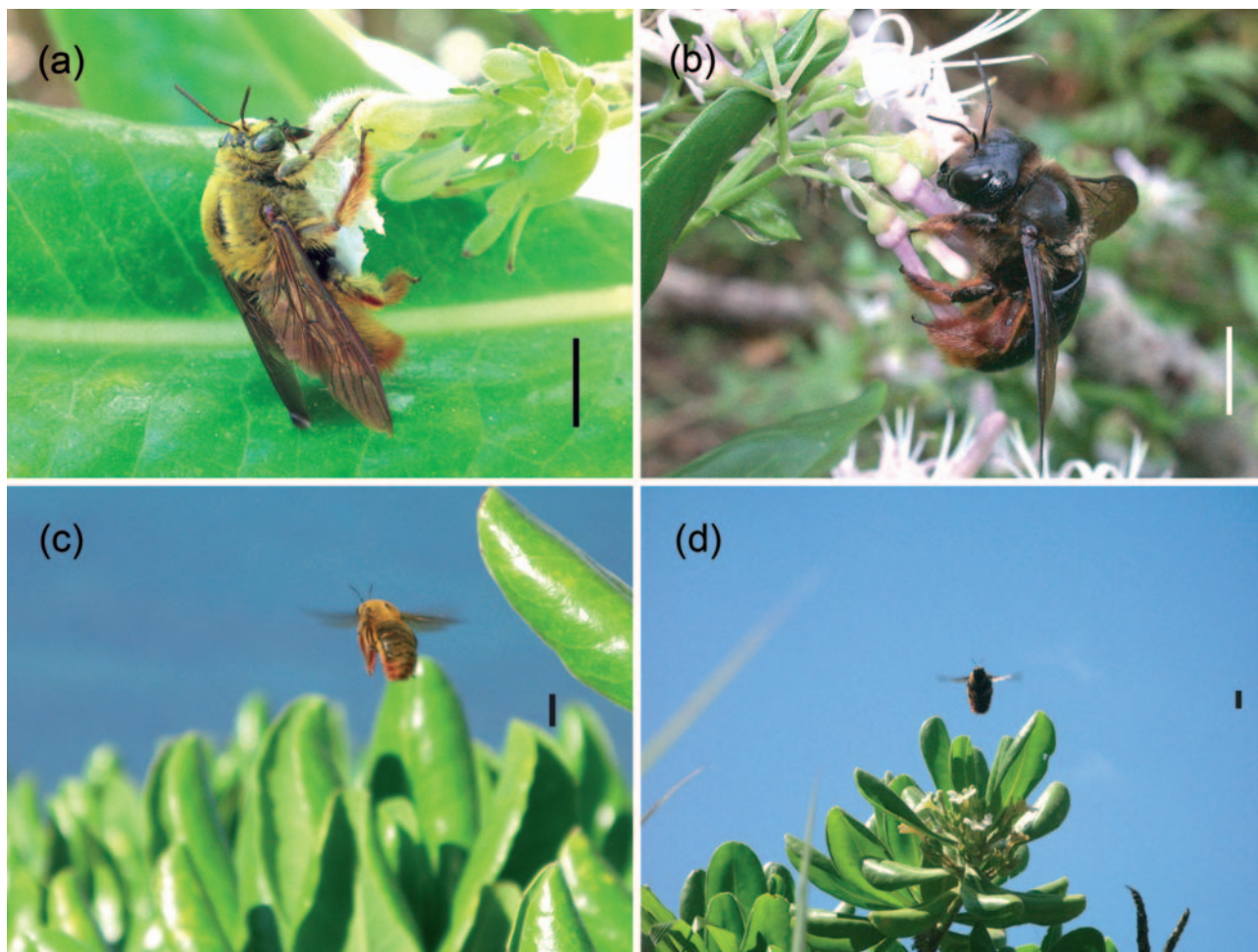


Fig. 1. Flower-visiting and territorial behaviour of *Xylocopa ogasawarens*. (a) Male visiting a *Scaevola sericea* flower. (b) Female visiting flowers of the endemic *Hedyotis leptopetala*. (c) Male patrolling *S. sericea* shrubs. (d) Male hovering and defending his territory around *S. sericea* inflorescences. Scale bars: 10 mm.

MATERIAL AND METHODS

Study site and species

The Ogasawara Islands are located in the northwestern Pacific Ocean approximately 1000 km south of the Japanese mainland (Shimizu, 2003). The endemic large carpenter bee *X. ogasawarens* is the only species of the genus and the largest bee found on the islands (Sakagami, 1961; Ohbayashi et al., 2003). Male and female *X. ogasawarens* are easily distinguished in the field by their conspicuous sexual dimorphism (as in other species of the subgenus *Koptortosoma*), the coloration of males is yellowish (Fig. 1a) and that of females brownish (Fig. 1b; Sakagami, 1961). As in other species of *Xylocopa*, each female of *X. ogasawarens* makes a single nest by digging a hole in the dead branches of trees. Nest-site searching and nesting behaviour of females are frequently observed on the islands in May–July (Goubara, 2002; Sugiura, unpubl. data).

Methods

The territorial behaviour of *X. ogasawarens* males on flowers of a native plant species, *Scaevola sericea* Vahl (Campanulales: Goodeniaceae), was observed at Samegasaki, a coastal area on Hahajima (Fig. 1c; 26°38'N, 142°09'E; elevation 2–9 m). The vegetation at this coastal site was mainly composed of *S. sericea* shrubs. The height of the *S. sericea* ramets ranged from 0.25 to 2.1 m and the flowers developed from the axillary buds of shoots. To determine the significance of male

territorial behaviour, *S. sericea* shrubs growing along a trail 30 m in length were observed for about 8 h on five sunny days: 15:15–16:30 on 1 July; 9:30–10:30 and 16:00–17:00 on 2 July; 8:50–10:00 and 16:20–16:50 on 3 July; 8:45–9:45 and 15:40–16:40 on 4 July; and 8:25–9:35 on 5 July 2007. No *X. ogasawarens* individuals were observed from 10:30 to 15:00 on flowers of *S. sericea* on any day. Three categories of male behaviour were recorded: nectar-feeding (Fig. 1a), territoriality (Fig. 1c, d) and resting.

The time spent defending territories (i.e., hovering and patrolling near flowers) by territorial males at the site was recorded to the nearest second with a stopwatch ($n = 17$). When males left their territories, the height and distance from inflorescences of male hovering sites was measured to the nearest 10 mm using a tape measure ($n = 30$). To determine whether male bees choose inflorescences with the greater number of flowers, the number of flowers between defended ($n = 18$) and randomly selected inflorescences ($n = 18$) were compared on 4 July. A generalized linear model (GLM) with Poisson error distribution was used to test the difference (JMP ver. 6.0; SAS Institute, 2005). When males attacked other males in the defence of their territories, I recorded whether or not the territorial males were successful ($n = 25$). This behaviour was observed from a short distance from their territories (ca. 3–5 m).

To clarify the relationship between flowers visited by females and the territorial behaviour by males, I collected flower-

TABLE 1. Records of flower-visiting behaviour by *Xylocopa ogasawarensis* by plant species.

Family	Species	Status ²	Life form	Time of flowering	Sexes of <i>X. ogasawarensis</i>	References
Asteraceae	<i>Helianthus annuus</i>	Cultivated	Herb	May	Female	Ogasawara, pers. obs.
Campanulaceae	<i>Lobelia boninensis</i>	Endemic	Herb	May–Nov.	Female	Kato et al., 1999; Goubara, 2002; Abe, 2006
Clusiaceae	<i>Calophyllum inophyllum</i>	Indigenous	Tree	Jun.–Sep.	Female/Male ³	Abe, 2006; Wada, pers. obs.
Compositae	<i>Dendrocacalia crepidifolia</i>	Endemic	Tree	Nov.–Dec.	Female	Goubara, 2002
Convolvulaceae	<i>Ipomoea pes-caprae</i> subsp. <i>brasiliensis</i>	Indigenous	Herb	Jun.–Dec.	Female/Male	Abe, 2006; Sugiura, unpubl. data
Elaeocarpaceae	<i>Elaeocarpus photiniaefolius</i>	Endemic	Herb	Jun.–Aug.	Female	Goubara, 2002
Fabaceae	<i>Leucaena leucocephala</i>	Alien	Tree	Jun.–Dec.	Female	Wada, pers. obs.; Kawazoe, pers. obs.
Fabaceae	<i>Canavalia lineata</i>	Indigenous	Herb	May–Aug.	Female	Goubara, 2002; Kawazoe, pers. obs.
Goodeniaceae	<i>Scaevola sericea</i>	Indigenous	Shrub	May–Oct.	Female/Male ³	Kato, 1992; Abe, 2006; this study
Malvaceae	<i>Hibiscus glaber</i> ¹	Endemic	Tree	Jun.–Dec.	Female	Kato, 1992; Abe, 2006; Sugiura, unpubl. data
Malvaceae	<i>Hibiscus tiliaceus</i> ¹	Indigenous	Tree	Jun.–Dec.	Female	Tanaka, 1991
Melastomataceae	<i>Melastoma tetramerum</i>	Endemic	Shrub	Jul.–Sep.	Female	Goubara, 2002; Abe, 2006
Melastomataceae	<i>Melastoma tetramerum</i> var. <i>pentapetalum</i>	Endemic	Shrub	Jul.–Aug.	Female	Abe, 2006
Myrtaceae	<i>Metrosideros boninensis</i>	Endemic	Tree	Aug.–Oct.	Female	Abe, 2006; Sugiura, unpubl. data
Myrtaceae	<i>Syzygium cleyerifolium</i>	Endemic	Tree	Jul.	Female	Wada, pers. obs.
Palmae	<i>Clinostigma savoryanum</i>	Endemic	Tree	Jun.–Aug.	Female	Sugiura, unpubl. data
Ranunculaceae	<i>Clematis boninensis</i>	Endemic	Vine	Jul.–Nov.	Female	Abe, 2006
Rosaceae	<i>Rubus nakaii</i>	Endemic	Shrub	Apr.–May	Female	Nagata, 2003
Rubiaceae	<i>Hedyotis leptopetala</i>	Endemic	Shrub	Jul.–Dec.	Female	Abe, 2006; Sugiura, unpubl. data
Theaceae	<i>Schima mertensiana</i>	Endemic	Tree	Mar.–Jun.	Female/Male ³	Kato, 1992; Abe, 2006; Sugiura, unpubl. data; Wada, pers. obs.
Verbenaceae	<i>Callicarpa subpubescens</i>	Endemic	Tree	Apr.–Aug.	Female	Kawakubo, 1998
Verbenaceae	<i>Stachytarpheta jamaicensis</i>	Alien	Herb	Feb.–Dec.	Female	Wada, pers. obs.
Zingiberaceae	<i>Alpinia boninsimensis</i>	Endemic	Herb	Jun.–Jul.	Female	Abe, 2006

¹Nectar of the plant is robbed by *X. ogasawarensis*; ²Indigenous: nonendemic native; ³Males observed hovering near flowers.

visiting records of *X. ogasawarensis* from previous studies. When the sex of the individuals visiting flowers was not recorded, I asked the investigators for this information. Furthermore, I collected the flower-visiting records of *X. ogasawarensis* from several investigators and local naturalists. The species and sex can easily be identified by anyone in the field because of the large size of the species and this sexual colour dimorphism (Fig. 1a, b). Status (cultivated, alien, endemic, or nonendemic native), life forms (herb, vine, shrub, or tree), and flowering periods (months) of each plant species visited by *X. ogasawarensis* were obtained from Toyoda (2003) and Abe et al. (2004).

RESULTS

I observed 80 independent periods of territorial behaviour by *X. ogasawarensis* males. Although several of these observations may be for the same males, 3–5 males were observed hovering at the same time on each study day. Males hovered 239 ± 75 mm (mean \pm SD) away from inflorescences (Fig. 1c, d) 887 ± 325 mm above the ground and circled (patrolled) around the inflorescences.

The maximum diameter of the territories ranged from about 0.5 to 2.0 m, although it could not be accurately measured. Time spent defending territories ranged from 29 to 873 s (mean \pm SD, 331 ± 256 s). Some hovering males were frequently observed

touching the defended inflorescences momentarily, suggesting that they marked their own territories with a secretion. The number of open flowers did not differ between male-defended and randomly selected inflorescences [GLM, $df = 1$, $\chi^2 = 0.026$, $P = 0.87$; median (range), defended, 3 (2–7) vs. randomly selected, 3 (1–9)]. Thus, territorial male bees did not choose inflorescences of *S. sericea* with the greatest number of flowers.

Territorial males were frequently observed to attack other males that invaded their territories and/or fed on the nectar of defended flowers. Each territory-defending male made a direct frontal attack on an invading male and chased it out of its territory (c.f., Linsley, 1965; Barrows, 1983). At least 80% of the territorial interactions between males resulted in the successful defence by the territorial holder and at least 4% resulted in the loss of the territory; other outcomes could not be successfully determined. Nectar-feeding honeybees (the introduced *Apis mellifera* L.) were observed visiting flowers defended by *X. ogasawarensis* males on two occasions; neither territorial male defended its territory against these flower-visitors and did not chase the honeybees away.

Thirteen and 3 independent periods of nectar-feeding by males and females, respectively, were observed at the study site. Both males and females took nectar from undefended *S. sericea* flowers. Three males were observed resting on leaves of *S. sericea*, suggesting that males may not be active from 10:30 to

15:00 during the day, although females were seen flying to their nests or searching for nest sites in the forest.

The flower-visiting behaviour of *X. ogasawarensis* is recorded for at least 23 plant taxa (Table 1). Most flower-visiting behaviour is documented for females, with only four plant species reported for males (Table 1). Male hovering behaviour was observed around flowers of three plant species: *Schima mertensiana* (Siebold & Zuccarini) Koidz. (Theaceae), *Calophyllum inophyllum* Linnaeus (Clusiaceae) and *S. sericea*. The flowering periods of these species coincide with the provisioning period of *X. ogasawarensis* (May–July).

DISCUSSION

Territorial behaviour of the males of the genus *Xylocopa* is generally related to mate searching and mating behaviour (e.g., Gerling et al., 1989). Flowers are important encounter sites for male and female bees (Eickwort & Ginsberg, 1980). Flower-based territorial behaviour of male bees is recorded in *Xylocopa* species (Gerling et al., 1989), as well as in several solitary bee species (Alcock et al., 1978; Severinghaus et al., 1981; Sugiura et al., 2007). *Xylocopa ogasawarensis* males hovered near inflorescences of the native plant species *S. sericea*, patrolled around them and defended the area against other males (Fig. 1d). Therefore, *X. ogasawarensis* males hold a resource-based (flowers) territory. Because different types of male territorial behaviour are reported even within the same species of bees including *Xylocopa* (Leys, 2000; Paxton 2005), *X. ogasawarensis* males may also display other types of territorial behaviour such as nonresource territoriality or other resource-based, e.g., nest site territoriality.

Females of *X. ogasawarensis* are polylectic (generalists) as they visit the flowers of many plant species (Table 1). Males of polylectic bees may mate at other sites than flowers (e.g., nest sites), because they are less likely to encounter mates on a given food plant than males of oligolectic (specialist) bees. However, females of *X. ogasawarensis* mainly visit flowers of a few plant species during the provisioning period, e.g., *Schima mertensiana* and *Scaevola sericea* in June (Sugiura, unpubl. data). The nest sites that females frequently search for or return to are sparsely distributed in forests. Thus, *X. ogasawarensis* males can more easily find flowers than nest sites during the provisioning period (May–July; Table 1). Mating in many species of bee occurs in the male's territory, although different mating sites are reported even within the same species (reviewed by Paxton, 2005). Therefore, flower-based territorial behaviour in *X. ogasawarensis* males appears to be closely associated with searching for mates and/or mating, although mating in *X. ogasawarensis* has not been observed.

Males of *X. ogasawarensis* frequently attacked and drove other males from their territories. However, males did not defend their territories against flower-visitors of other species (i.e., honeybees). *Xylocopa ogasawarensis* males did not chase other insects, unlike males of other *Xylocopa* species (Linsley, 1965; Barrows, 1983). Therefore, the male territorial behaviour of *X. ogasawarensis* may be related to intrasexual competition for sites visited by females.

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