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AN INVERTEBRATE PERSPECTIVE TO HUTCHINSON'S RATIO USING CO-OCCURRING TIGER BEETLE (COLEOPTERA: CICINDELIDAE) ASSEMBLAGES

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Abstract
Tiger beetles co-occur for cryptic advantage, interspecific hybridization, reproductive synchrony and thermoregulation. Successful co-occurrence relies on the absence of competition and Hutchinson (1959) has proposed body size ratios for co-occurrence of bird and mammal taxa. The present study calculates body size ratios for co-occurring tiger beetle assemblages and investigates similarities with ratios for co-occurring birds and mammals. Ratios obtained using measurements of different morphological characters are considered and compared. Association of body size ratios of co-occurring tiger beetles with habitat type and number of species in co-occurring tiger beetle assemblage are determined. The study revealed a body weight ratio and body length ratio for co-occurring tiger beetles that was similar to Hutchinson's ratios for birds and mammals. Different ratios were obtained when using different morphological parameters. Body size ratios inferred using mandible lengths differed significantly according to habitat type. Further, relatively higher values were observed for assemblages occupying terrestrial habitats while lower values were found for assemblages of aquatic habitats.

Keywords**:** body size, competition, morphology, habitat type, Sri Lanka

Introduction

Many animals "co-occur" in multispecies assemblages in various ecosystems. Biotic interactions such as beneficial hybridization (Chunco *et al*., 2012), heterospecific attraction where heterospecifics indicate the suitability of a habitat (Sebastian-Gonzalez *et al.*, 2010), aggregation effect of native species occurring in communities invaded by other species (Sanders *et al.*, 2003) and the rich diversity of foods available in an ecosystem (Thorington & Ferrell, 2006) are known to foster co-occurrence amongst many taxa. However, co-occurrence leads to competition that results in loss of species (Westman & Savolainen, 2001), juvenile bottlenecks (Guruge & Amarasinghe, 2008), non-detection of certain species that leads to conservation issues (Bailey *et al.*, 2009) and predation (Taggart *et al.*, 2005). Therefore, competition and other unfavourable conditions should be absent for successful co-occurrence to prevail. In 1959, Hutchinson suggested that for ecologically similar species to co-occur a constant ratio between body sizes must persist (Hutchinson, 1959; Simberloff & Boecklen, 1981; Weins, 1982; Eadie *et al.*, 1987). By the examination of birds and mammals he suggested an average ratio (larger/smaller) of 1.3 for body length and 2.0 for body weight (Weins, 1982; Eadie *et al.*, 1987). Many studies further demonstrated the use of other morphological measurements – skull length, head width, bill length, jaw length, carapace width, ovipositor length, proboscis length, wing length – for calculation of this average ratio (Weins, 1982). However, as the measurements of different morphological characters produced different ratios, and in some cases different size-sequence structuring for similar morphological characters in different species, the ecological relevance of the characters used need to be considered (Weins, 1982).

Tiger beetles (Coleoptera, Cicindelidae) are omnivorous predators that occur in temperate and tropical environments. Many adult tiger beetles co-occur and are found as sympatric assemblages of two to fifteen species in a range of habitats (Cornelisse & Hafernik, 2009). Ten species of tiger beetles co-occur on flats and stream banks of the Eastern Nebraska salt marsh of which one species is a threatened insect in the United States (Hoback *et al.*, 2001). Eight species co-exist on the floodplains of the Tedori River System of Japan (Satoh *et al.*, 2006). Three species co-exist as a communal roost on plant species of Simbalbara Wildlife Sanctuary, Shivalik Hills, India (Bhargav & Uniyal, 2008). Four species of tiger beetles are found on the river beds of Arkavathy and Cauvery river, Karnataka, India (Ganeshaiah & Belavadi, 1986), and two species occur sympatrically in the mountain habitats of Colombia (Tigreros & Kattan, 2008). In Japan, nine species of tiger beetle co-occur in estuarine seashore and sand dunes along the coast (Satoh *et al.*, 2003).

Studies of co-occurring tiger beetles have concentrated on niche partitioning of species according to preferences for prey, vegetation, temperature, soil characteristics and oviposition choice (Ganeshaiah & Belavadi, 1986; Hoback *et al.*, 2000; Woodcock *et al.*, 2010). Further, co-existence as a communal roost has been related with cryptic advantage, thermoregulation and synchrony of reproduction and dispersal (Bhargav & Uniyal, 2008). Interspecific hybridization in co-occurring tiger beetle species (Brust *et al.*, 2012), as well as reproductive isolation in some cases of sympatric species (Tigreros & Kattan, 2008) have also been addressed. Satoh *et al*. (2003) investigated body size differences in co-occurring coastal tiger beetle species assemblages in Japan. The study considered the head width and mandible length of species and relative overlaps between species were calculated. However, the ratios proposed by Hutchinson (1959) have not been calculated for co-occurring tiger beetle species and whether the patterns adhere to the values envisioned by Hutchinson has not been considered. If ratios adhere to the proposed ratios they can be used to support Hutchinson's ratio from an invertebrate perspective and further, as evidence for absence of competition.

Therefore, in the present study we calculated body size ratios for co-occurring tiger beetle assemblages using morphometric data that have been recorded in previous studies and current study conducted in Sri Lanka. Ratios obtained using measurements of different morphological characters were considered and compared. Association of body size ratios of co-occurring tiger beetles with habitat type and association of body size ratios with number of species in co-occurring tiger beetle assemblage were determined. Further, co-occurring tiger beetle populations of Sri Lanka were investigated and species assemblages, locations and habitat types recorded. The study aimed to detect a pattern in size relationships of co-occurring tiger beetle species and whether body size ratios can be used as an index to suggest co-existence of species.

Materials and methods

***Compilation of data from previous studies*:** Data on co-occurring tiger beetle species was obtained from nine studies conducted from 1979 to 2010. Co-occurring species, locations, habitat types and body size ratios obtained from morphometric measurements were recorded for tiger beetle assemblages reported in the studies (Appendix 1). Body size ratios (larger species over the smaller one) for co-occurring species were calculated using morphometric data: body weight; body length, from the frons of head to the elytral apex; head width, maximum width including eyes; mandible gape, the space between open mandibles; mandible length, distance between articulation point and the tip of the mandible; and elytral length, distance between base of scutellum and apex of elytra. When an assemblage consisted of more than two species, ratios were calculated by considering the association of each species with every other species.

***Investigation and collection of tiger beetles from Sri Lanka*:** Investigations for tiger beetles were conducted in ninety-four locations of Sri Lanka from May 2002 to December 2006. Coastal areas, river banks, reservoir banks, agricultural lands, marsh lands and urban areas were investigated in the wet, intermediate and dry zones of the country. When beetles were encountered a sample of three to five beetles of each species was collected using a standard insect net and preserved in 70% alcohol for identification. Permission to make collections of tiger beetles was obtained from the Department of Wildlife Conservation, Sri Lanka.

***Identification of tiger beetles*:** Tiger beetles were identified using keys for *Cicindela* (*sensu lato*) of the Indian subcontinent (Acciavatti & Pearson, 1989) and descriptions of Horn (1904), Fowler (1912) and Naviaux (1984). Identifications were confirmed by comparing the specimens with type specimens available in the National Museum of Colombo, Sri Lanka and British Natural History Museum of London, United Kingdom. Nomenclature is based upon Wiesner (1992) except for the use of *Calomera* Motschulsky, 1862 instead of *Lophyridia*, based upon Lorenz (2005).

***Measurement of morphological parameters of tiger beetles*:** Co-occurring tiger beetle assemblages were identified and the body weight, body length and mandible length were measured and recorded for each specimen. Body weight was estimated by weighing each beetle to the nearest mg on an analytical balance (Chyo JL180, Chyo Balance Corp., Japan). Body length was estimated by measuring the distance from the frons of the head to the elytral apex when the head was in the normal feeding position. Caudal spines on the elytral apex were disregarded (Acciavatti & Pearson, 1989). Mandible length was estimated by measuring the distance from the articulation point to the tip of the left mandible. Broken and worn out mandibles were disregarded (Pearson & Juliano, 1991). Measurements of both body length and mandible length were taken using a dissecting microscope (Nikon Corporation SE, Japan) with an eyepiece graticule (Nikon, Tokyo, Japan) that was calibrated by an objective micrometer (Olympus, Japan).

***Data analysis*:** Body size ratios obtained from different morphological characters were compared using One-Way Analysis of Variance and Tukey's Multiple Comparison method of the Minitab 16.0 statistical software package. Association between habitat type and mandible length ratios of co-occurring tiger beetle assemblages, and association between number of co-occurring species in an assemblage and mandible length ratios were analyzed using the same test and software. The sample size for mandible length ratios was large when comparing with ratios obtained for other morphological data. Therefore, they were utilised in the analysis for demonstrating the association between body size ratios and habitat type and association between body size ratios and number of co-occurring species in an assemblage.

Results

***Information obtained from previous studies and current study*:** Data consisted of a total of sixty-four tiger beetle assemblages of which fifty-eight assemblages were from previous studies and six assemblages were from Sri Lanka. Each assemblage consisted of two to twelve tiger beetle species. Co-occurring assemblages were recorded from five distinct habitat types – Coastal (sand dunes, salt flats, sea shores, beaches and bays), Reservoir (Pond edges), Grassland, Forest (open forests, rain forests) and River (creeks, water canals, floodplains). Tiger beetle assemblages of Sri Lanka were recorded from reservoir and river bank habitats, and consisted of two to three species accounting for a total of seven species (Appendix 1).

***Body size ratios of co-occurring tiger beetle assemblages*:** Three hundred and fifty-eight (358) body size ratios were calculated for the sixty-four assemblages of co-occurring tiger beetles (Appendix 1). Body size ratios differed according to the morphometric parameter considered. Ratios obtained using body length, head width and mandible lengths were not statistically different, while body weight ratio was not statistically different to mandible gape ratio. A significant statistical difference was evident between body length, head width, mandible length ratios and body weight, mandible gape ratios ($p < 0.01$, $F = 10.32$) (Table 1).

Table 1: Body size ratios of co-occurring tiger beetle assemblages; means sharing a common letter(s) are not significantly different according to Tukey's Multiple Comparison test.

Morphometric character	Body size ratio
Body weight (*n*=10)	1.83[a] ±1.1
Mandible gape (*n*=21)	1.85[a] ±0.7
Body length (*n*=15)	1.26[b] ±0.2
Head width (*n*=51)	1.26[b] ±0.2
Mandible length (*n*=260)	1.37[b] ±0.3
Elytral length (*n*=1)	1.04[c]

***Mandible length ratios and habitat type*:** Significant differences were evident between mandible length ratios of co-occurring tiger beetles in different habitat types. Ratios for terrestrial habitat types (grasslands, forests) were significantly larger than the ratios for aquatic habitat types (reservoir, riverine, coastal). The largest mandible length ratios were obtained for tiger beetle assemblages of grassland habitats, while the smallest ratios occurred in species of reservoir habitats ($p < 0.01$, $F=11.00$) (Fig. 1; Table 2).

Table 2: Mandible length ratios of co-occurring tiger beetle assemblages in different habitat types; means sharing a common letter(s) are not significantly different according to Tukey's Multiple Comparison test.

Habitat type	Mandible length ratio
Coastal (*n*=78)	1.39[a] ±0.03
Riverine (*n*=30)	1.40[a] ±0.05
Reservoir (*n*=76)	1.22[b] ±0.03
Grassland (*n*=26)	1.67[c] ±0.09
Forest (*n*=51)	1.42[d] ±0.05

***Mandible length ratios and number of co-occurring species*:** A clear relationship was not evident between mandible length ratio and number of tiger beetle species in an assemblage. The smallest ratios were observed in assemblages consisting of 12 species, while the largest ratios were seen in assemblages consisting of 6 species ($p < 0.01$, $F = 8.43$) (Table 3).

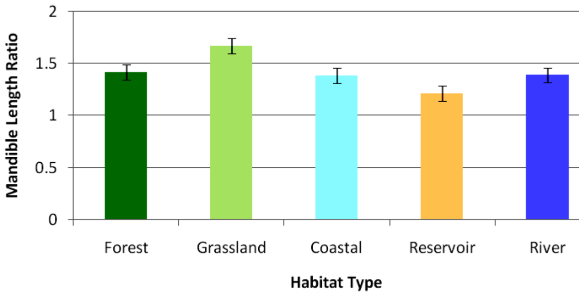

Figure 1: Mandible length ratios of co-occurring tiger beetle assemblages in different habitat types

Table 3: Relationship between mandible length ratios and number of co-occurring tiger beetle species; means sharing a common letter(s) are not significantly different according to Tukey's Multiple Comparison test.

Number of species in an assemblage	Mandible length ratio
Two (*n*=24)	1.38[a] ±0.05
Three (*n*=51)	1.52[b] ±0.04
Four (*n*=66)	1.38[a] ±0.04
Five (*n*=40)	1.30[c] ±0.05
Six (*n*=15)	1.67[d] ±0.13
Twelve (*n*=66)	1.22[c] ±0.03

Discussion

The analysis of body size ratios of co-occurring species has been a major focus in evolutionary ecology. Hutchinson concluded that this value could be used as an indication of the kind of difference necessary to permit two species to co-occur in different niches but at the same level of a food-web. A body size ratio of 1.3 for body length and 2.0 for body weight was interpreted as the amount of separation necessary to permit co-occurrence of species at the same tropic level. Larger organisms preferring larger prey relative to smaller prey makes it necessary that similar size species must be more widely separated avoiding minimum size ratios, while large ratios in assemblages result in more severe competition amongst species (Weins, 1982). The present study revealed an average body weight ratio of 1.83 and an average body length ratio of 1.26 for co-occurring tiger beetle assemblages. These ratios were closely similar to the ratios suggested by Hutchinson (body weight = 2.0, body length = 1.3) for co-occurring birds and mammals. Therefore, it is possible that the values proposed by Hutchinson in 1959 for vertebrate taxa may be applicable for invertebrates as well. However, consideration of other co-occurring invertebrate taxa in addition to tiger beetles is required to confirm this finding. Body size ratios of tiger beetles differed according to the morphological measurement under consideration and mandible gape ratios were statistically similar to body weight ratios while head width and mandible length ratios were statistically similar to body length ratios. Thus, the present investigation infers that co-occurring tiger beetles have body size ratios of 1.26 – 1.37 when using body length, head width and mandible length, while ratios of 1.83 – 1.85 are obtained when using body weight and mandible gape.

Co-occurring tiger beetle assemblages of different habitat types demonstrated different mandible length ratios which were larger for terrestrial habitat types (grasslands, forests) and smaller for aquatic habitat types (rivers, coastal areas, reservoirs). This illustrated that species with a wide range of sizes can be expected in terrestrial assemblages while species with a narrower range of sizes can be expected in aquatic assemblages. Body size of tiger beetles is specific to habitat type (Dangalle *et al.*, 2013). Large species are specific to reservoir and coastal habitats, while small species occupy riverine habitat types (Dangalle *et al.* 2013). Such associations can narrow the body size ranges of taxa occupying a habitat and result in smaller body size ratios. The present study revealed body size ratios for tiger beetle assemblages of reservoir habitats to be significantly small. This is strongly possible due to the high significance of body size – habitat type relationship of tiger beetles recorded from reservoir habitats (Edirisinghe *et al.*, 2014). However, the relationships of tiger beetle body size with terrestrial habitats such as forests and grasslands have not been investigated. The large body size ratios revealed in the present study indicates the possibility of species assemblages with a wide range of body sizes for these habitat types.

According to Pearson and Vogler (2001), if three or fewer species of tiger beetles co-occurred, the ratio of their mandible lengths is greater than 1.3. Similarly, in the present investigation a mandible length ratio greater than 1.3 occurred in tiger beetle assemblages consisting of two and three tiger beetle species. However, a consistent association between mandible length ratio and number of co-occurring tiger beetle species was not evident as larger ratios occurred in assemblages of four and six species, and ratios less than 1.3 occurred in assemblages of five and twelve species.

When considering the co-occurring tiger beetles of Sri Lanka species were found on large sandy banks of river and reservoir habitat types. *Calomera angulata* (Fabricius, 1798) was the main species in sympatric assemblages and was found in five of the six associations. Further, recent investigations in May 2014 revealed *C. angulata* co-occurring with another tiger beetle species in a riverine habitat at Deduru Oya, Puttalam District. *C. angulata* has also been recorded in co-occurring tiger beetle assemblages of riverine habitats of India and coastal habitats of Japan. In Sri Lanka, it is the main species of reservoir habitats (Dangalle *et al.*, 2012) and according to the present investigation the main species of sympatric tiger beetle assemblages.

Our study reveals that co-occurring tiger beetle species display body weight and body length ratios similar to the ratios proposed by Hutchinson (1959) for birds and mammals. Ratios can be obtained using different morphological characters, and mandible gape ratios of tiger beetles are similar to body weight ratios, while mandible length and head width ratios are similar to body length ratios. Mandible length ratios of co-occurring tiger beetle assemblages in terrestrial habitats are larger than for tiger beetles of aquatic habitats, which may be due to the close association of body size of tiger beetles with aquatic habitat types. Further investigations in terrestrial habitats are required for more accurate inferences.

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Appendix I: Data for co-occurring tiger beetles

Location	Co-occurring species	Body weight ratio	Body length ratio	Mandible length ratio	Mandible gape ratio	Head width ratio	Elytral length ratio	Source
Pond edge, Sulphur Springs Valley, Arizona, USA	*Cicindela haemorrhagica* *Cicindela marutha* *Cicindela ocellata* *Cicindela pimeriana* *Cicindela praetextata* *Cicindela punctulata* *Cicindela sedecimpunctata* *Cicindela tenuisignata* *Cicindela viridisticta* *Cicindela nevadica* *Cicindela nigrocoerulea* *Cicindela willistoni*			1.02, 1.16, 1.02, 1.06, 1.22, 1.04, 1.06, 1.88, 1.06, 1.14, 1.07, 1.19, 1.04, 1.04, 1.25, 1.06, 1.09, 1.92, 1.08, 1.17, 1.04, 1.14, 1.23, 1.05, 1.12, 1.10, 1.62, 1.10, 1.02, 1.24, 1.08, 1.22, 1.02, 1.04, 1.85, 1.04, 1.12, 1.08, 1.10, 1.30, 1.13, 1.99, 1.12, 1.21, 1.00, 1.18, 1.15, 1.54, 1.16, 1.07, 1.30, 1.02, 1.81, 1.02, 1.10, 1.11, 1.78, 1.00, 1.08, 1.13, 1.78, 1.65, 2.00, 1.08, 1.13, 1.21				Pearson & Mury (1979)

Location	Co-occurring species	Body weight ratio	Body length ratio	Mandible length ratio	Mandible gape ratio	Head width ratio	Elytral length ratio	Source
Grassland, Sulphur Springs Valley, Arizona, USA	*Cicindela obsolete* *Cicindela pulchra* *Cicindela nigrocoerulea* *Cicindela horni* *Cicindela lemniscata* *Cicindela debilis*			1.02, 1.50, 1.36, 2.46, 2.25, 1.52, 1.38, 2.50, 2.29, 1.10, 1.65, 1.51, 1.81, 1.66, 1.09				Pearson & Mury (1979)
Arkavathy, Cauvery River Junction, Karnataka, India	*Cicindela cardoni* *Cicindela cancellata* *Cicindela sumatrensis* *Cicindela minuta*		1.17, 1.16, 1.80, 1.00, 1.55, 1.54	1.25, 1.09, 1.63, 1.36, 1.77, 1.30				Ganeshaiah & Belavadi (1986)
Carizzo Creek, Arizona, USA	*Cicindela tranquebarica*, *Cicindela oregona*	1.21						Schultz & Hadley (1987)
Sand dunes, Fox Valley, Canada	*Cicindela limbata* *Cicindela scutellaris* *Cicindela lengi* *Cicindela formosa*			1.15, 1.29, 1.47, 1.12, 1.27, 1.13				
Open forest, Pennsylvania, USA	*Cicindela purpurea* *Cicindela tranquebarica*			1.01				
	Cicindela scutellaris *Cicindela purpurea* *Cicindela patruela* *Cicindela tranquebarica*			1.01, 1.03, 1.05, 1.02, 1.04, 1.02				
Salt flat, New Mexico, USA	*Cicindela fulgida* *Cicindela togata* *Cicindela circumpicta* *Cicindela nevadica* *Cicindela willistoni*			1.20, 1.24, 1.30, 1.30, 1.03, 1.08, 1.08, 1.04, 1.05, 1.00				
Salt flat, Kansas, USA	*Cicindela togata* *Cicindela circumpicta* *Cicindela nevadica* *Cicindela fulgida* *Cicindela willistoni*			1.15, 1.22, 1.25, 1.29, 1.06, 1.08, 1.11, 1.02, 1.06, 1.03				
Grassland, Arizona, USA	*Cicindela lemniscata* *Cicindela nigrocoerulea* *Cicindela obsoleta*			1.63, 2.22, 1.36				Pearson & Juliano (1991)
	Cicindela obsolete *Cicindela horni*			1.26				
	Cicindela debilis *Cicindela horni* *Cicindela obsoleta*			1.73, 2.19, 1.26				
	Cicindela lemniscata *Cicindela nigrocoerulea* *Cicindela pulchra*			1.63, 2.35, 1.44				
Permanent pond edge, Arizona, USA	*Cicindela punctulata* *Cicindela ocellata* *Cicindela sedecimpunctata* *Cicindela haemorrhagica*			1.03, 1.17, 1.31, 1.13, 1.27, 1.12				
Temporary pond edge, Arizona, USA	*Cicindela marutha* *Cicindela fulgoris*			1.00				
Grassland, Chandigarh, India	*Cicindela lefroyi* *Cicindela striatifrons*			1.31				
Permanent pond edge, Chandigarh, India	*Cicindela melancholica* *Cicindela minuta*			1.46				

Location	**Co-occurring species**	**Body weight ratio**	**Body length ratio**	**Mandible length ratio**	**Mandible gape ratio**	**Head width ratio**	**Elytral length ratio**	**Source**
Sandy river bank, Chandigarh, India	*Cicindela albopunctata* *Cicindela subtilesignata* *Cicindela intermedia*			1.39, 1.21, 1.68				Pearson & Juliano (1991)
Sandy river bank, Chandigarh, India	*Cicindela agnate* *Cicindela venosa* *Cicindela angulata* *Cicindela chloris* *Cicindela plumigera*			1.12, 1.43, 1.49, 1.82, 1.28, 1.32, 1.62, 1.04, 1.27, 1.22				
Lowland rain forest, Karnataka, India	*Cicindela striolata* *Cicindela collicia* *Cicindela fabriciana*			1.74, 2.33, 1.34				Pearson & Juliano (1991)
Open forest, Karnataka, India	*Cicindela dasiodes* *Cicindela fastidiosa* *Cicindela bicolor* *Cicindela calligaramma* *Cicindela aurofasciata*			1.18, 1.84, 1.88, 2.28, 1.57, 1.60, 1.94, 1.02, 1.24, 1.21				
Sandy river edge, Karnataka, India	*Cicindela undulate* *Cicindela minuta* *Cicindela cancellata* *Cicindela angulata*			1.23, 1.35, 1.86, 1.10, 1.51, 1.38				
Highland rain forest, Kerala, India	*Cicindela belli* *Cicindela striolata* *Cicindela hamiltoniana* *Cicindela andrewesi*			1.71, 1.94, 2.14, 1.13, 1.25, 1.11				
Lowland rain forest, Heredia, Costa Rica	*Odontocheila iodopleura* *Odontocheila nicaraguensis*			1.56				
Lowland rain forest, Puntarenas, Costa Rica	*Odontocheila iodopleura* *Odontocheila chiriquina*			1.36				
Lowland rain forest, B.C. Island, Panama	*Odontocheila salvini* *Odontocheila chiriquina*			1.37				
Lowland rain forest, Napo, Ecuador	*Odontocheila trilbyana* *Odontocheila consobrina* *Odontocheila cayennensis*			1.39, 1.62, 1.17				
Lowland rain forest, Pichincha, Ecuador	*Odontocheila iodopleura* *Odontocheila chiriquina*			1.35				
Lowland rain forest, Ucayali, Peru	*Odontocheila rufiscapsis* *Odontocheila cayennensis*			1.33				
Lowland rain forest, Beni, Bolivia	*Odontocheila egregia* *Odontocheila spinipennis* *Odontocheila confusa*			1.08, 1.51, 1.40				
Lowland-terra rain forest, Tambopata, Peru	*Odontocheila luridipes* *Odontocheila annulicornis* *Odontocheila cayennensis*			1.21, 1.37, 1.14				
Lowland-floodplain rain forest, Tambopata, Peru	*Odontocheila lacordairei* *Odontocheila cyanella* *Odontocheila annulicornis* *Odontocheila confusa*			1.09, 1.34, 1.73, 1.23, 1.59, 1.29				
Open forest bamboo, Tambopata, Peru	*Odontocheila annulicornis* *Odontocheila chrysis*			1.07				
Lowland rain forest, Borneo, Indonesia	*Therates batesi* *Therates spinipennis*			1.63				

Location	**Co-occurring species**	**Body weight ratio**	**Body length ratio**	**Mandible length ratio**	**Mandible gape ratio**	**Head width ratio**	**Elytral length ratio**	**Source**
Lowland rain forest, Sepik, Papua New Guinea	*Therates rathschildi* *Therates festivus* *Therates basalis*			1.30, 2.05, 1.57				Pearson & Juliano (1991)
Sandy river bank, Kenya	*Cicindela nilotica* *Cicindela regalis* *Cicindela dongalensis*			1.54, 2.09, 1.35				
Salt Marsh, Eastern Nebraska, USA	*Cicindela circumpicta* *Cicindela togata*	2.02						Hoback *et al*. (2001)
Black Water Flood Plains, Manaus, Brazil	*Phaeoxantha lindemannae* *Phaeoxantha bifasciata* *Tetracha punctata* *Phaeoxantha limata*				1.33, 1.48, 2.33, 1.11, 1.75, 1.58			Zerm & Adis (2001)
White Water Flood Plains, Manaus, Brazil	*Phaeoxantha klugii* *Phaeoxantha aequinoctialis* *Tetracha punctata* *Tetracha spinosa* *Cylindera suturalis* *Pentacomia cribata*				1.44, 1.64, 1.94, 3.59, 3.28, 1.14, 1.35, 2.50, 2.29, 1.18, 2.19, 2.00, 1.85, 1.69, 1.09			
Sea Shore, Tanega-shima Island, Kagoshima, Japan	*Lophyridia angulata* *Abroscelis anchoralis* *Cylindera elisae* *Callytron yuasai*			1.32, 1.75, 1.85, 1.33, 1.41, 1.06		1.01, 1.28, 1.28, 1.26, 1.26, 1.00		Satoh *et al*. (2003)
Sea Shore, Shibushi Bay, Kagoshima, Japan	*Lophyridia angulata* *Myriochile speculifera* *Abroscelis anchoralis* *Cylindera elisae*			1.60, 1.47, 1.95, 1.09, 1.32, 1.22		1.06, 1.11, 1.39, 1.05, 1.25, 1.31		
Sea shore, Hyuga, Miyazaki, Japan	*Lophyridia angulata* *Abroscelis anchoralis* *Cylindera elisae*			1.42, 1.74, 1.22		1.11, 1.31, 1.17		
Sand dunes, Kaseda, Kagoshima, Japan	*Myriochile speculifera* *Lophyridia angulata* *Cylindera elisae*			1.43, 1.78, 1.24		1.02, 1.27, 1.30		
Fukiage beach, Kagoshima, Japan	*Cicindela lewisii* *Lophyridia angulata* *Cylindera elisae* *Callytron inspecularis*			1.18, 1.74, 1.94, 2.04, 2.29, 1.12		1.08, 1.48, 1.55, 1.37, 1.44, 1.05		
Sea shore, Sendai, Kagoshima, Japan	*Cicindela lewisii* *Callytron inspecularis*			1.95		1.52		
Sea shore, Ohzai, Ohita, Japan	*Cicindela lewisii* *Cylindera elisae*			1.66		1.42		
Sea shore, Nagasaki, Japan	*Cicindela lewisii* *Myriochile speculifera* *Callytron yuasai* *Cylindera elisae*			1.32, 1.64, 1.71, 1.24, 1.30, 1.04		1.09, 1.38, 1.48, 1.27, 1.35, 1.07		

Location	Co-occurring species	Body weight ratio	Body length ratio	Mandible length ratio	Mandible gape ratio	Head width ratio	Elytral length ratio	Source
Sea shore, Hiroshima, Japan	*Cicindela lewisii* *Cylindera elisae*			1.63		1.41		Satoh *et al*. (2003)
Sea shore, Tokoshima, Japan	*Cicindela lewisii* *Cylindera elisae*			1.66		1.45		
Sea shore, Shizuoka, Japan	*Chaetodera laetescripta* *Cylindera elisae*			1.52		1.47		
Sea shore, Ibaraki, Japan	*Chaetodera laetescripta* *Cylindera elisae*			1.58		1.52		
Sea shore, Shimane, Japan	*Lophyridia angulata* *Cylindera elisae*			1.76		1.30		
Sand dune, Tanegaike, Japan	*Lophyridia angulata* *Cicindela tranbaicalica* *Cylindera elisae*			1.31, 1.77, 1.35		1.14, 1.32, 1.15		
Tottori dune, Tottori, Japan	*Chaetodera laetescripta* *Lophyridia angulata* *Cylindera elisae*			1.24, 1.43, 1.74		1.05, 1.36, 1.30		
Sea shore, Ishikawa, Japan	*Lophyridia angulata* *Abroscelis anchoralis* *Cylindera elisae*			1.27, 1.75, 1.38		1.07, 1.34, 1.25		
Sea shore, Niigata, Japan	*Chaetodera laetescripta* *Lophyridia angulata* *Cicindela transbaicalica* *Cylindera elisae*			1.20, 1.00, 1.52, 1.21, 1.83, 1.52		1.07, 1.15, 1.48, 1.07, 1.38, 1.29		
Western Andean Range, Colombia	*Pseudoxycheila confuse* *Pseudoxycheila chaudoiri*						1.04	Tigreros & Kattan, (2008)
Beach ridge, Wapusk National Park, Manitoba	*Cicindela l. longilabris* *Cicindela limbata hyperborea*		1.25					Woodcock *et al*. (2010)
Water canal, Handapangoda, Kalutara district, Sri Lanka	*Cylindera* (*Ifasina*) *willeyi* *Cylindera* (*Ifasina*) *waterhousei*	1.04	1.08	1.00				Dangalle *et al*. (unpublished data)
Devahuwa wewa, Dambulla, Sri Lanka	*Cylindera* (*Oligoma*) *lacunose* *Lophyra* (*Lophyra*) *catena* *Calomera angulata*	4.17, 3.56, 1.17	1.41, 1.45, 1.03					
Kandalama wewa, Dambulla, Sri Lanka	*Myriochila* (*Monelica*) *fastidiosa* *Calomera angulata*	1.14	1.05	1.17				
Tabbowa wewa, Karuwalagaswewa, Sri Lanka	*Myriochila* (*Monelica*) *fastidiosa* *Calomera angulata*	1.03	1.01	1.01				
Ma Oya, Alawwa, Sri Lanka	*Calomera cardoni* *Calomera angulata*	1.77	1.25	1.19				
Nachchaduwa wewa, Anuradhapura, Sri Lanka	*Myriochila* (*Monelica*) *fastidiosa* *Calomera angulata*	1.21	1.12					