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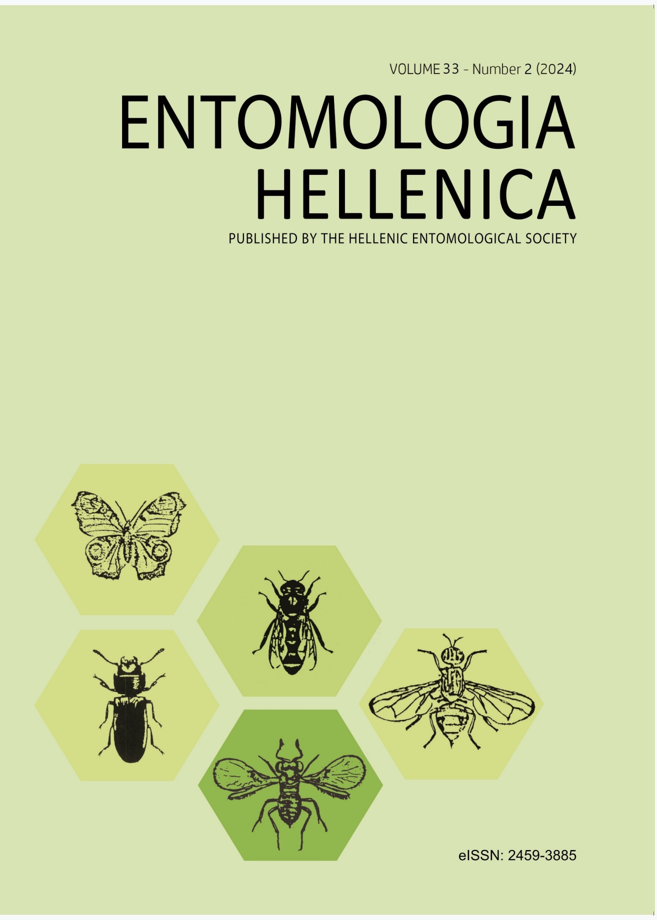

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Feeding Categorisation of some Caeliferan and Ensiferan species (Insecta: Orthoptera) collected from selected grasslands in Sendai City, Japan

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ABSTRACT

Although orthopteran species have often been regarded as polyphagous herbivores, most of them show variable degrees of diet selectivity and particular food preferences. Still some species possess peculiar feeding categories which need further investigation. An assemblage of 43 orthopteran species, 7 families, 12 subfamilies and 13 tribes was surveyed from five grasslands in Sendai City, Japan to investigate their feeding preferences and were classified into seven main feeding categories based on examination of morpho-mandibular characteristics and postmortem gut content analyses. The forbivorous category was the most dominant, whereas the herbivorous the least common.

KEY WORDS: Orthoptera, mandibular characteristics, gut contents analysis, feeding categories.

Introduction

Orthopterans have emerged as a crucial group of invertebrates for environmental monitoring and assessment. The Orthoptera order, comprising a diverse array of species, holds a prominent position amongst insect orders (Zhang 2011; Bidau, 2014). With approximately 28,000 identified species worldwide and ranked as the sixth largest order in Class Insecta, trailing only the Hemiptera order as declared by Cigliano et al. (2022). Species belonging to Orthoptera are present in every terrestrial environment and exhibit remarkable diversity (ElEla et al., 2010; Yadav and Kumar 2017).

Taxonomists classified Orthoptera into two distinct suborders: Ensifera, encompassing crickets, katydids, and their relatives, and Caelifera, which include grasshoppers and their allies (Song, 2018). Orthopteran species play considerably vital roles in terrestrial food webs, serving as a valuable protein source for various animals, including amphibians, birds, small reptilian species, as well as some mammalian species. Consequently, their scarcity could disrupt the delicate trophic structure within an ecosystem (Soliman et al., 2017). They play a central role in food webs, as they are mostly primary herbivores and constitute an abundant food resource for other groups of carnivorous organisms (Parr and Chown, 2003). The composition of orthopteran assemblage is considerably highly responsive to environmental changes, play a crucial role in the ecosystems function and can serve as a valuable environmental

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indicator (O’Neill et al., 2003). Indeed, these species potentially serve as useful bioindicators for land disturbance (Saha et al. 2011) providing valuable insights into qualities of ecosystems and the effectiveness of ecological networks (Zhang et al., 2019).

Orthopteran species have attracted significant attention due to the extensive damage they inflict by their herbivory action on crops and various forms of green vegetation (Dakhel et al., 2020). Aspects of feeding strategies, including selection of food, preference of food, diverse feeding patterns and diet specialization have been studied by many researchers for diverse orthopteran species (e.g., Isely, 1944; Williams, 1954; Mulkern, 1967; Otte and Joern, 1976; Bernays and Chapman, 1978; Uvarov, 1977; Ohabuike, 1979, Joern; 1983, 1985; Bernays and Bright, 1993, ElSayed, 2005; ElShazly and ElSayed, 2006; ElEla et al., 2010, 2012; Kuřavová and Kočárek, 2016; ElSayed et al., 2020).

Adaptation to food intake has led to behavioral and morphological specialization of mouthparts (Snodgrass, 1935). Fry et al. (1978) found that caeliferan species, especially Acridomorpha, are often phytophagous, and the adaptations of their mandibular structures are associated with different types of food and different species of ecological groups of plants, grasses, forbs, flowers, and seeds (Isely, 1944; Patterson, 1983, 1984; Kang and Chen, 1994; Bernays, 1998; Gangwere et al. 1998; ElEla, 2011; ElEla et al. 2010, 2012; Di Russo et al. 2014; Kuřavová and Kočárek, 2016; ElSayed et al. 2020).

Considering the paucity of information on the assemblage of orthopteran species inhabiting the five selected grasslands in Sendai city, especially on the variation of mandibles in accordance with food preference, our team was stimulated to examine the morpho- mandibular variations of orthopteran species and evaluate the gut contents analysis as evidence supporting these morpho-adaptations. Moreover, there is a lack of information regarding the diet of tetrigid species which are relatively among the least-studied groups of Orthoptera (Flook and Rowell, 1997; Hochkirch et al. 2000 & 2006) especially those recorded in some parts of Asia (Song et al. 2015) and more specifically from Sendai City, Japan (ElEla et al. 2010).

Materials and Methods

Climate and topography. The study was carried out in Sendai City, Japan (lat. 38°16'05" N, long. 140°52'11" E). The area of the city is ca. 788.09 km^2 and stretches from the Pacific Ocean to the Ōu Mountains, which are the east and west borders of Miyagi Prefecture. As a result, the geography of the city is quite diverse. Eastern Sendai is a plain, the center of the city is hilly, and western areas are mountainous.

According to the Japan Meteorological Agency (http://www.data.jma.go.jp), meteorological records showed that Sendai City has a humid subtropical climate, which features warm and wet summers, and cool and dry winters. The summer season starts in June and ends at the end of September with significant seasonal variations in temperature and rainfall. Summers are warm, with an August average temperature of 24.1 °C and the majority of the annual precipitation is delivered during summer.

The city is rarely hit by typhoons, and experiences only 6 days with more than 10 centimeters of precipitation on average.

Monsoon season usually begins in late April to early October, which is later than in most cities in Japan. During this season, cold winds from the Okhotsk air mass, which are called “Yamase”, blow in and depress daytime highs.

Extremes of temperature degrees range from −11.7 to 37.2 °C and Sendai City experiences fewer days of extreme temperatures (highs outside 0 – 30 °C at 19.6 days/year compared to Tokyo's average of 49 days/year.

Winters are cool and relatively dry, with the January temperature averaging at 1.5 °C. Concerning snow, snowfalls are much lower than at the cities on the Sea of Japan coast, such as Niigata and Tottori (Climate data for Sendai normals, extremes [1926−present], Japan Meteorological Agency, http://www.data.jma.go.jp).

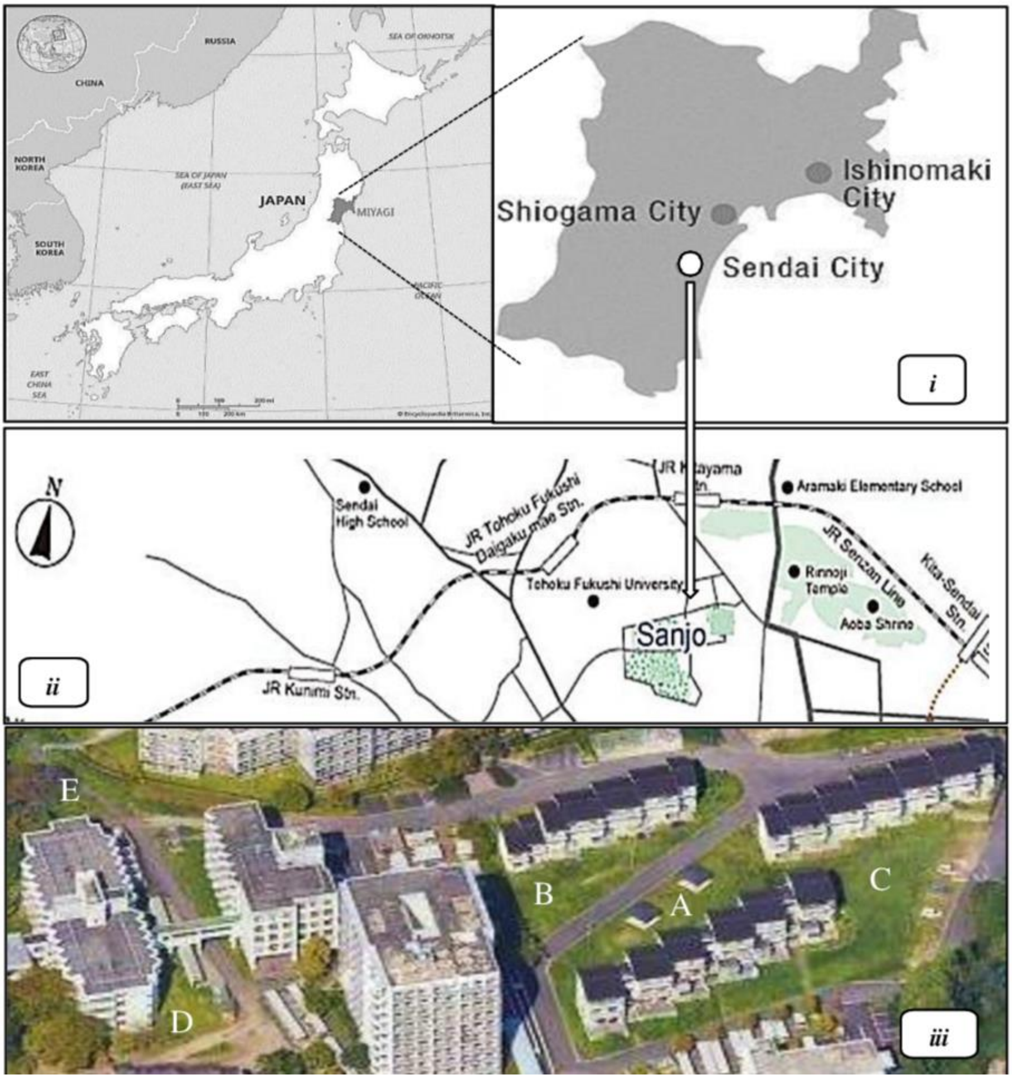

FIG. 1.**:** Map of the study site: (*i*) Map of Japan showing Miyagi Prefecture and Sendai City, Japan, (*ii*) Map of Sanjo-machi with the grassland plots (*iii*) aerial photograph showing the five grassland plots within Sanjo-machi (marked by white capital letters). (Source: Tohoku University https://www.tohoku.ac.jp/english/profile/campus/01/access/)

Study site. The study site comprised of five main plots of grasslands (Fig. 1). Grassland A and B were longitudinal, L-shaped transects, covered by short and long grasses, with a presence of several shrubs. Grassland C was adjacent to a parking lot. It was a longitudinal quadrate plot covered by short grasses, with long grasses on the edges. Grassland D was a T-shaped plot, with a canopy almost dominated by relatively short grasses. Grassland E was almost trapezoid with very few trees scattered all over (Fig. 1). The canopy was composed of mixed grasses and diverse flowering plant species. A small bond was located at the northern edge and was surrounded by long grasses.

In general, on analyzing the selected sampling sites for their floral composition, it was found comparatively rich with several, wildly grown, monocot and dicot species. The most dominant grass species was Bermuda grass, *Cynodon dactylon* (L.).

The five selected grasslands were almost intact, not subjected to any kind of land-use effects, reclaiming or being influenced by severe anthropogenic stresses. The grasslands were only mowed twice per year, the first mow being undertaken after the end of Spring (during the last week of April) and the second at the beginning of Autumn (during the first week of November) and before initiation of snow falls. Each mow lasted 2-3 days for all five grasslands. It should be noted that a negative effect on Orthoptera presence due to mowing (Humbert et al. 2010; Cizek et al. 2012; Chisté et al. 2016) was not possible since sampling was performed during a period not associated with the post-mowing period, as orthopterans start to appear at the end of June and completely disappear by the beginning of October.

Sampling protocol. Orthopteran assemblage was collected from the study sites, from the beginning of July until the end of September, over two consecutive years, 2022 and 2023, using standard sweep net. Concerning the time effort per unit, the sampling schedule was adjusted to be performed between 1000 and 1400 h. To minimize the bias in sampling, only one of the researchers was responsible for sampling the individuals of different orthopteran species. The collected individuals were promptly killed in the field and stored in proper sampling containers. Details of the sampling technique are given by ElEla (2011).

The collected specimens were brought to the laboratory for systematic identification using the key of Ichikawa et al. (2006). Individuals of different orthopteran species were counted, sorted and kept in individually marked clean glass vials for further analyses. Additional identified specimens were stored individually in secure vials which then freezed (- 25 ◦C).

Feeding category. Feeding categories of different orthopteran species were elucidated from mandibular morphological characteristics and compared with previous reports, when information data was available. Laboratory dissections were followed immediately after bringing the collected specimens to the lab. Mandibles of adult orthopterans were exposed by lifting the labrum and hauling the maxillae. The mandibles were lightly brushed with 80% ethyl alcohol and distilled water to remove adhering debris (ElSayed, 2005; Smith and Capinera, 2005). Mandibles were then carefully detached from the head capsule by loosening the abductor muscles connecting the mandibles to the head capsule by regular and gentle back and forth hauling of each mandible using forceps, under a stereomicroscope (Olympus SZX12, Hamburg, Germany). Mandibles were then examined at 20-40x magnification, under direct illumination and photographs were taken from both ventral and dorsal views of each mandible with a digital camera (Sony HDR-CX590V, Japan). Morpho- mandibular characteristics were carefully examined and recorded in attempts to predict the feeding category of each orthopteran species.

Due to the rather wide gap in the relative abundance amongst orthopteran species, five adult male individuals from each species were subjected to gut contents analysis (total n = 215). As in many instances, females of certain orthopteran species feed more often than males (Hochkirch, 1999), it is necessary to clarify that only males were processed in the analyses since food strategies often differ between sexes, where it has been shown that females could consume plant species richer in nutrients (Chapman, 1990) and fertilized females tend to consume more protein, so even in purely herbivorous species, arthropod remains in the gut could appear during this period for relatively higher demand in protein requirements for production of eggs (ElSayed, 2005). For species with more than five adult males, the five individuals were randomly selected among collected males.

Adult male individuals of the collected orthopteran species were dissected by dissecting scissors and the alimentary tract was exposed, then longitudinally opened and the contents of the gut were permanently mounted on a glass microscope slides (Mulkern and Anderson, 1959; Brusven and Mulkern, 1960; Ohabuike, 1979; Kang and Chen, 1994; LeGall et al., 1998, 2003; ElSayed, 2005; ElSayed et al., 2020). Drops of distilled water wereadded whenever required to minimize dryness of the collected gut contents. These slides were examined under a light binocular microscope (Olympus® CX41RF, Hamburg, Germany) at 40× magnification. Microscopic examinations of fragments including different plant species (monocots and dicots), arthropod body parts and/or other ingested matters including debris particles were performed (Kang and Chen, 1994; ElSayed, 2005; ElEla et al. 2010; ElSayed et al. 2020).

Qualitative records of the gut contents were made following ElEla et al. (2010) and ElSayed et al. (2020) to categorize each orthopteran species into a proper feeding category. The proposed seven feeding categories were:

1. Herbivorous feeders (H): The frequency of fragments of dicots species ≅ frequency of fragments of monocots species with absence of fragments from arthropod parts.
2. Herbivorous-mixed feeders (Hm): the same as herbivorous category with arthropod parts recorded in the gut.
3. Graminivorous feeders (G): Frequency of fragments of monocots species exceeding 75% of the gut contents and no arthropod matter detected.
4. Forbivorous feeders (F): Frequency of fragments of dicots species exceeding 75% of the gut contents with absence of fragments from arthropod parts.
5. Forbivorous-mixed feeders (Fm): resembles the forbivorous category with arthropod parts recorded in the gut.
6. Mixed-feeders (M): plant matters (including roots, tubers and subterranean parts) and arthropod and/or earthworm (Oligochaeta) parts encountered in almost equal proportions.
7. Detrito-bryophagous feeders (Db): detritus, mosses, algae and lichens were mainly encountered in the gut beside other plant matters.

Results

Taxonomic composition

The entire study area, for all five sites pooled, a total of 43 species (28 and 35 in 2022 and 2023, respectively), representing 25 genera, 7 families, 12 subfamilies and 13 tribes (Table 1) were recorded over the two consecutive years. The total number of collected individuals was 988 and 1324 during 2022 and 2023, respectively. The most dominant orthopteran species was *Atractomorpha lata* (Mochulsky, 1866). Overall, five orthopteran species were dominating the assemblage. These species were *A. lata* (Mochulsky, 1866), *Conocephalus maculatus* (Le Guillou, 1841), *Loxoblemmus equestris* (Saussure, 1877), *Mecopoda niponensis* (Haan, 1843), *Acrida cinerea* (Thunberg, 1815) (Table 1). These species constituted 59.72% of the total assemblage during 2022 and 52.34% of the total assemblage during 2023 (Table 1). The sex ratio varied considerably among the different species and even between years (Table 1). Moreover, an absence of males or females of relatively rare species, e.g. *Locusta migratoria* (Linnaeus, 1758) and *Loxoblemmus tsushimensis* (Ichikawa, 2001) was recorded, as well as the absence of both sexes of other species e.g. *Euconocephalus varius* (Walker, 1869) during a specific year, 2022, was also recorded (Table 1).

Feeding category

Based on the observations of the variability of mandibular characteristics and analysis of contents of the alimentary canal, seven different feeding categories were identified (Table 1). Out of 43 recorded species sampled over the study period, 12 species (ca. 27.91%) were mixed-feeders (M) (Table 1).

Gryllidae and Trigonididae showed mandibles with comparatively sharp incisors and relatively long knife-shape terebral ridge. These mandibular characteristics could delineate a predacious feeding behavior. Based on postmortem gut content analyses, guts of dissected species showed fragmentary parts of plant materials including roots, occasionally debris matters and subterranean arthropod body parts. Consequently, the feeding category of these eight species could be positioned in the mixed-feeding category (M).

On the second rank of our recorded feeding categories, nine detrito-bryophagous feeders (Db), which comprised approximately 20.93% of the categories, were recorded in all tetrigid species (Table 1). Dissected guts of these species showed peculiar contents in which their guts were mainly loaded with detritus, algal parts, mosses and fungal hyphae.

Graminivorous (G) and forbivorous-mixed feeders (Fm) were positioned in the third rank (ca. 16.28% for each category). The main graminivorous feeders frequently showed mandibular abrasions (Fig. 2). Both incisor and molar areas were subjected to obvious mechanical wear as a result of feeding habit, as is the case for *Acrida cinerea* (Thunberg, 1815) (Fig. 2).

On the other hand, species which are members in Conocephalini and Mecopodini were forbivorours-mixed feeders (Fm) where the incisor area was prominent and robust comprising a comparatively larger portion of the mandible and was associated with sharp terebral ridge (Fig. 2). In comparison, the molar area was small with two short and parallel molar slats.

Three species were forbivorous (F) in which the mandibular characteristic features were associated with the processing of forb resources (Table 1). The incisor area is equipped with robust and sharp teeth. The molar area consists of a small molar ridge forming a trituration area with molar slats for grinding forbs thoroughly (Fig. 2). The gut content analyses of these species showed that the contents were loaded with irregular fragments of forbs.

The three Phaneropterini species, *Hexacentrus japonicus* (Karny, 1907), *Phaneroptera nigroantennata* (Brunner von Wattenwyl, 1878) and *P. falcate* (Poda, 1761) were herbivourous-mixed feeders (Hm), with prominent and sharp incisors, without prominent wearing, and a comparatively smaller molar area (Fig. 2).

TABLE 1. Orthopteran species collected from the study sites in Sendai, Japan, with their families, subfamilies, tribes, number of individuals and their feeding category.

Family	**Subfamily**	**Tribe**	**Orthopteran species**	**No. of individuals (♂:♀)**		**Feeding category***
				2022	**2023**	
Acrididae	Acridinae	Acridini	*Acrida cinerea* (Thunberg, 1815)	54 (23: 31)	47 (19:28)	G
			A. conica (Fabricius, 1781)	33 (18:15)	39 (24:15)	G
	Melanopilinae	Podismini	*Parapodisma mikado* (Bolivar, 1890)	0	11 (8:3)	F
	Oedipodinae	Aiolopini	*Aiolopus thalassinus tamulus* (Fabricius, 1798)	23 (10:13)	10 (6:4)	H
		Locustini	*Oedaleus infernalis* (Saussure, 1884)	10 (3:7)	19 (12:7)	G
			Locusta migratoria (Linnaeus, 1758)	0	7 (5:2)	G
			Gastrimargus marmoratus (Thunberg, 1815)	0	9 (5:4)	G
	Oxyinae	Oxyini	*Oxya japonica* (Thunberg, 1815)	12 (4:8)	22 (15:7)	G
			O. yezoensis (Shiraki, 1910)	0	8 (5:3)	G
Pyrgomorphidae	Pyrgomorphinae	Atractomorphini	*Atractomorpha lata* (Mochulsky, 1866)	308 (131:177)	458 (168:290)	F
			A. sinensis (Bolivar, 1905)	0	14 (8:6)	F
Tetrigidae	Tetriginae	Tetrigini	*Euparatettix tricarinatus* (Bolívar, 1887)	13 (8:5)	0	Db
			Formosatettix niigataensis (Storozhenko & Ichikawa, 1993)	0	15 (7:8)	Db
			Tetrix akagiensis (Uchida & Ichikawa, 1991)	13 (9:4)	0	Db
			T. japonica (Bolivar, 1887)	21 (15:6)	29 (13:16)	Db
			T. kantoensis (Uchida & Ichikawa, 1991)	29 (18:11)	28 (14:14)	Db
			T. larvatus (Bei-Bienko & Mishchenko,1951)	16 (6:10)	37 (16:21)	Db
			T. macilenta (Ichikawa, 1993)	18 (6:12)	22 (14:8)	Db
			T. minor (Ichikawa, 1993)	7 (2:5)	0	Db
			T. silvicultrix ichikawa (Ichikawa, 1993)	20 (6:14)	21 (12:9)	Db
Eneopteridae	Oecanthinae	Oecanthini	*Oecanthus similator ichikawa* (Ichikawa, 2001)	12 (6:6)	0	F
			Loxoblemmus aomoriensis (Shiraki, 1930)	23 (9:14)	48 (22:26)	M

Gryllidae	Gryllinae	Gryllini	*L. equestris* (Saussure, 1877)	68 (39:29)	69 (45:24)	M
			L. tsushimensis (Ichikawa, 2001)	0	12 (7: 5)	M
			L. sylvestris (Matsuura, 1988)	6 (5:1)	0	M
			Teleogryllus emma (Ohmachi & Matsuura, 1951)	0	12 (5:7)	M
			T. infernalis (Saussure, 1877)	8 (2:6)	20 (6:14)	M
			Trigonidium pallipes (Stål, 1861)	7 (7: 0)	0	M
			Velarifictorus aspersus (Walker, 1869)	0	7 (5:2)	M
			V. mikado (Saussure, 1877)	43 (17:26)	90 (36: 54)	M
			V. ornatus (Shiraki, 1911)	14 (8:6)	0	M
Tettigoniidae	Conocephalinae	Conocephalini	*Conocephalus maculatus* (Le Guillou, 1841)	75 (43:32)	94 (59:35)	Fm
			C. melaenus (Haan, 1843)	21 (14:7)	14 (5:9)	Fm
			C. japonicus (Redtenbacher, 1891)	0	9 (6:3)	Fm
			Euconocephalus varius (Walker, 1869)	0	11 (8:3)	Fm
			Ruspolia dubia (Redtenbacher, 1891)	0	12 (10:2)	Fm
			R. lineosa (Walker, 1869)	38 (22:16)	59 (27:32)	Fm
	Mecopodinae	Mecopodini	*Mecopoda niponensis* (Haan, 1843)	85 (39:46)	25 (7:18)	Fm
	Phaneropterinae	Phaneropterini	*Hexacentrus japonicus* (Karny, 1907)	0	11 (7:4)	Hm
			Phaneroptera falcate (Poda, 1761)	0	20 (15:5)	Hm
			P. nigroantennata (Brunner von Wattenwyl, 1878)	0	8 (6:2)	Hm
Trigonididae	Nemobiinae	Pteronemobiini	*Dianemobius furumagiensis* (Ohmachi & Furukawa, 1929)	0	7 (5:2)	M
			Pteronemobius fascipes (Walker, 1869)	11 (6:5)	0	M
			Total number of individuals (♂:♀)	**988 (476:512)**	**1324 (632:692)**	

*Feeding category: Db: Detrito-bryophagous feeder, F: Forbivorous feeder, Fm: Forbivorous-mixed feeder, G: Graminivorous feeder, H: Herbivorous feeder, Hm: Herbivorous-mixed feeder M: Mixed feeder.

Table (1) showed that only one acridid species, *Aiolopus thalassinus tamulus* (Fabricius, 1798), possessed a purely herbivorous feeding category (H) which comprised approximately the least proportions of the total categories (ca. 2.33%). The incisor and molar areas were almost of uniform proportions. The incisors were parallel and sharp with no clear abrasions either in molar or incisor areas of the mandible (Fig. 2).

It was clear that the major differences in mandibular structure were related to differences in feeding behavior rather than the taxonomic position of the species as family Acridinae and Tettigoniidae possessed more than feeding category (Table 1).

Discussion

In the majority of phytophagous insect orders, Chapman (1982) noted that oligophagy or monophagy was observed in more than 50% of the species whereas the Orthoptera, stand apart from the other orders, more than 60% of the species have been classified as polyphagous and 25% as graminivorous (Picaud et al. 2003).

Orthopteran species are considered as one of the more diverse taxa with thousands of extant described species possessing prominent diversity in forms and habitats (Grimaldi and Engel, 2005; Bidau, 2014; Eades et al. 2014; Song et al. 2015) and representing crucial links in food chains (Badenhausser, 2012). Orthopteran species are widespread and important herbivores in natural grassland ecosystems and agro-ecosystems as they consume a considerable portions of grasses and forbs (Köhler et al. 1987, Blumer and Diemer 1996; ElSayed, 2005; Bharamal and Koli 2014) and regulate plant community structure (Zhang et al. 2011). Indeed, Order Orthoptera plays an influential and functional role in the recycling and equilibrium of natural ecosystems by enhancing the conversion of biomass through their easily transformable excrement (Samways, 1994; Hao et al. 2015; Ngoute et al. 2021). All the previous aspects triggered the urge to study the variations in feeding categories of different orthopteran species through mandibular morpho- characteristic variations and gut contents analysis rather than relying on field or laboratory observations or food choice tests.

The aspects of food strategies including selection of food, feeding patterns, food preferences, specialization in dietary requirements have been studied by many authors in a diverse orthopteran species (e.g., Williams, 1954; Gangwere, 1961; Mulkern, 1967; Otte and Joern, 1976; Bernays and Chapman, 1978; Uvarov, 1977; Joern, 1983, 1985; Bernays and Bright, 1993). Still the food strategy based on the structure of the mouthparts, habitat preferences, or feeding behavior was observed in only a few species (ElSayed et al. 2020).

Morphological variations in mouthparts, including mandibles, were subjected to further thorough research and itemized investigations have been directed by numerous authors in various regions, significant among them were Snodgrass (1928), Gangwere (1965, 1966), Gangwere et al. (1976, 1998) and Patterson (1984), Smith and Capinera (2005) in North America, Liebermann (1968), Gangwere and Ronderos (1975) in South America, Williams (1954); Kaufmann (1965), Gangwere and Morales (1973) in Europe, Gangwere and Spiller (1995); Gangwere et al. (1998) in the Mediterranean islands, Gapud (1968), Feroz and Chaudhry (1975), Kang et al. (1999), ElEla et al. (2010, 2012), ElSayed et al. (2020) in Asia, Chapman (1964), Le Gall et al. (1998, 2003) and ElSayed (2005) in Africa.

The strong relationship with diet makes morphological characteristics of mouthparts an important trait for insect evolutionary biologists (Snodgrass, 1928; Brues, 1939) and systematists (Mulkern, 1967). One of the first who coped with this topic was Isely (1944) who studied the de-

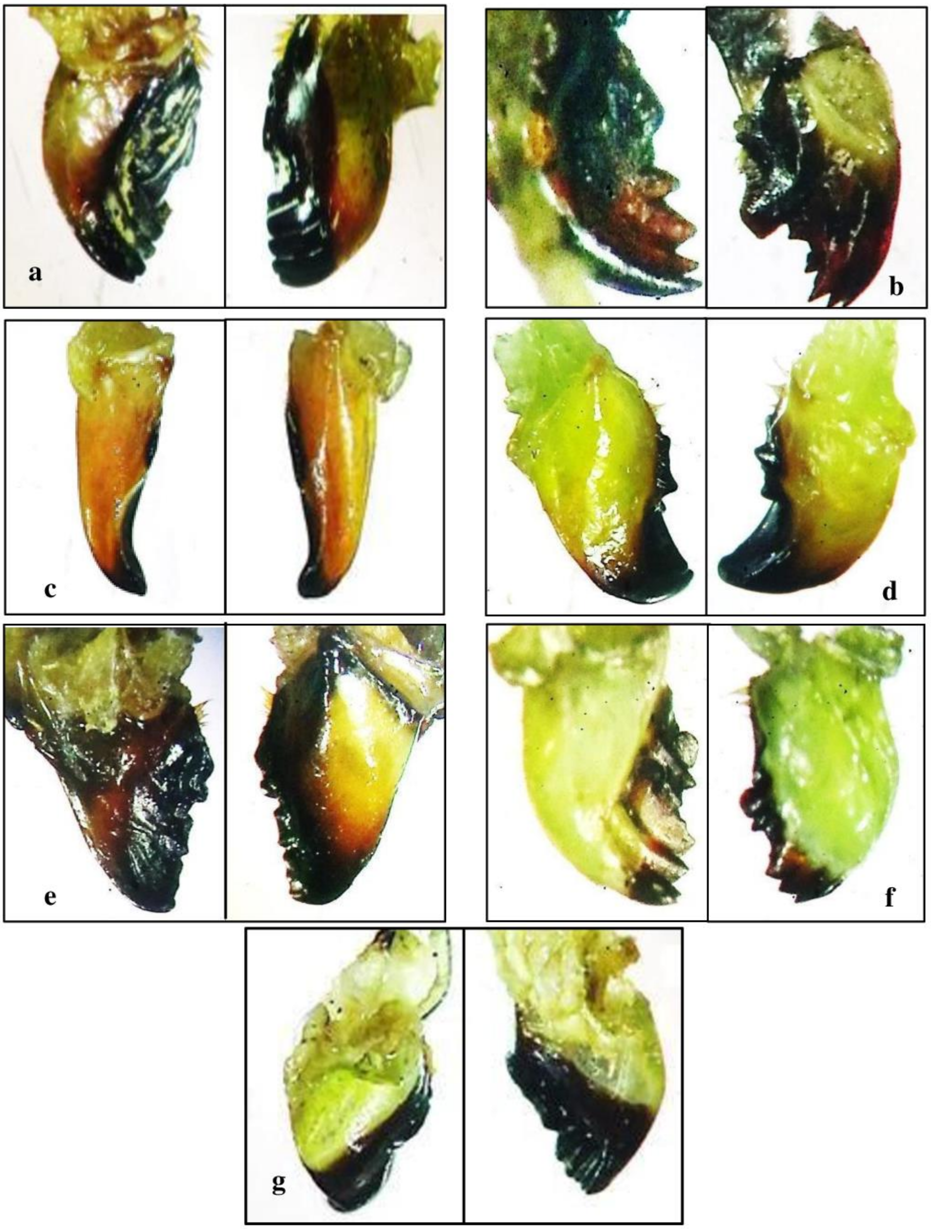

FIG. 2.**:** Images of morpho-mandibular variability representing different feeding categories. a. *Tetrix japonica* (Bolivar, 1887), a representative of Forbivorous species (F); b. *Hexacentrus japonicus* (Karny, 1907), a representative of Herbivourous-mixed species (Hm); c. *Conocephalus melaenus* (Haan, 1843), a representative of Forbivorous-mixed species (Fm); d. *Velarifictorus mikado* (Saussure, 1877), a representative of Mixed-feeder species (M); e. *Aiolopus thalassinus tamulus* (Fabricius, 1798), a representative of Herbivorous species (H); f. *Acrida cinerea* (Thunberg, 1815), a representative of Graminivorous species (G).

tailed morphological and structural features of mouthparts and correlated these characteristics with various feeding habits. Initial results and information offered by Isely (1944) on categorizing mandibles according to mandibular groups have since been shown to be prevalent, especially, in grasshoppers and other entomological taxa.

Isely (1944), on his research on 89 species, proclaimed two extreme forms of mandibles, i.e. graminivorous and forbivorous, with a series of intermediate forms associated with a mixed diet. Generally, Isely (1944) defined three groups of mandibles according to the overall structure and distinctive diet: (i) graminivorous (grass feeding type) with molar area adapted for grinding and incisors typically merged into a scythe like edge, (ii) forbivorous(forb or broad leaf plant feeding type) having a molar area composed of a depression encircled by elevated teeth and a strong interlocking incisor, (iii) herbivorous (mixed- feeding type) that have features of both of the previously mentioned groups.

On the other hand, Joern (1979) proposed that orthopteran species possess a broad spectrum in diversity of diet and consequently feeding behavior ranged from strict specialist to extreme generalist.

In accordance, several researchers (Gangwere, 1965; Chapman, 1990; Smith and Capinera, 2005) agreed with Isely (1944) and they had merely classified three main categories based on the plant categories. These categories were graminivorous, forbivorous and herbivorous (mixed-feeding). However, due to variations in mandibular morpho-characteristics, other studies provided broader classification of feeding categories (Kuřavová and Kočárek, 2016; ElEla et al. 2010; ElSayed et al. 2020).

Comparisons were performed by Patterson (1983) concerning the morphological structure of the mandibles with their niche variations. Hypothesis of niche variations predicts greater overall mandibular characteristic variability in orthopteran species having relatively the broadest trophic niches. In this study, mandibular characteristics of orthopteran species vary in different groups and these variations are therefore believed to meet the different feeding habits and in correspondence specifying a definite feeding category. These were in accordance with findings of several studies (Gangwere, 1965; ElEla, 2011; ElSayed et al. 2020).

Apparent observed similarities among members belonging to the same subfamily and striking differences between subfamilies assume a strong phylogenetic component to feeding adaptations as suggested by Otte and Joern (1977) and Joern (1979).

Ensiferan species, on the other hand, feeding categories ranged from forbivorous category which was observed in a single eneopterid species to strictly mixed feeding category. Ensiferans tended to feed on taxonomically diverse plant species (Palmer et al. 2024) beside frequent proportions of arthropod parts which could suggest predaceous or cannibalistic habits where some ensiferan species specialized on rather unusual food sources (ElEla, 2010; ElSayed et al. 2020).

The consumption of a specific diet is commonly associated with the shape and structure of the mandibles. Graziella et al. (2015) showed significant differences in the shapes of the mandibles among the variant forms of grasshopper species which may be due to the role of trophic diversification in the morphological differentiation of insect. The apparent diverse variations among mandibular characteristic features of different orthopteran species were remarkable to consider. In our research, more types of mandibles were suggested in association with analyses of gut contents in an attempt to position each collected species in the proper feeding category.

Although orthopteran species have often been regarded as polyphagous herbivores (ElSayed et al. 2020), most of these species show degree of dietary specialization (Mulkern, 1967; Uvarov, 1977; ElSayed et al. 2020). Orthopteran species possessed a dietary specialization was reflected in patterns of mandibular variations, and yet this diversification in morpho-mandibular characteristics could be utilized to catalogue orthopteran species in proper feeding category.

In this study, caeliferan species were strictly not engaged in cannibalistic behavior as confirmed by the absence of arthropod parts in their guts. However, other studies have recorded cannibalistic behavior in some caeliferan species only under crowded conditions (Bomar and Lockwood, 1994; ElEla, 2010).

It was interesting to spot the light on the peculiar detrito-bryophagy which was restricted to the tetrigid species with mosses, algal hyphae and debris matters were frequently encountered in their guts (Kuřavová and Kočárek, 2016).

Studies performed on tetrigids are considerably rare and restricted to a few species (Paranjape and Bhalerao, 1985; Blackith and Blackith, 1987; Reynolds et al. 1988; Hochkirch et al. 2000, Gröning et al. 2007; Kuřavová and Kočárek 2015; Kuřavová and Kočárek, 2016; Musiolek and Kočárek 2016), and even fewer and fragmentary in Japan (ElEla et al. 2010; ElEla, 2011; Tan et al. 2017; ElSayed et al. 2020).

The feeding habit of Tetrigidae has been described, ranging from observational to quantitative data, in only a few species (Tan et al. 2017). However, the detrito-bryophagy has been observed in almost all species (Verdcourt, 1947; Paranjape and Bhalerao, 1985; Hochkirch et al., 2000; Bidau, 2014; Kuřavová and Kočárek, 2015).

In a related species, *Tetrix undulata* (Sowerby, 1806), Verdcourt (1947) performed the faecal analysis and found a variety of mosses species in 80% of the fecal pellets. Lock (1996) analyzed crop content of three specimens of *T. subulata* (Linnaeus, 1758) and observed the presence of algae, detritus and sand grains with no traces of mosses or higher plants. Dietary habit of *T. undulata* (Sowerby, 1806) was studied by Hodgson (1963) and he observed feeding of the species on grasses (monocots), mosses (variety of species), lichens and algae, and on humus. Besides that, he observed also feeding on the dead bush cricket *Pholidoptera griseoaptera* (De Geer, 1773) in insectarium. Further studies were conducted by Hochkirch et al. (2000) who found that males of *T. undulata* (Sowerby, 1806) were exclusively feeding on mosses and algae, while females also included grasses and forbs in their diet. On other related tetrigid species, Reynolds et al. (1988) studied the diet of two tropical tetrigids in Sulawesi by analyzing their crop contents and they observed the presence of mosses or vascular plants in 82% of specimens of *Scelimena celebica* (Bolivar, 1887) and in 100% of specimens of *Diotarus pupus* (Bolivar, 1887). Indeed, it is far from precise to extend the detrito-bryophagy among all members of Tetrigidae since more documentation of dietary preference for each species is required in different spots and among different sexes.

Feeding category could be considered as an additional important ecological trait used to analyze the structure of orthopteran fauna. The collected orthopteran species were relatively dominated by forbivorous (F) and mixed (M) feeding species. However, mixed-feeding habit also comprised a relatively major percentage in the feeding categories of the assemblage.

Although Min and Min (2008), in their taxonomic studies, mentioned that *Aiolopus thalassinus* is an important graminivorous pest on different plants and grasses; our results from mandibular structure and gut contents analysis revealed a forbivorous feeding category for this species.

Comparisons in our research have shown that orthopteran species of the family Acrididae exhibited the broadest trophic niches with three feeding categories which support diverse patterns of mandibular characteristics and dietary preferences. Herbivorous and forbivorous species with mixed feeding habits (Hm and Fm) have more complex mandibular characteristics and relatively more heterogeneous food intake. These associations, in regard of morphological characteristics and dietary preference in each group, support Patterson's niche variation hypothesis Patterson (1983).

Possibly, species with mixed feeding categories (M, Fm and Hm) circumvent the defense systems by feeding only small portions of many plant species and other organic parts thus keeping the toxic levels of secondary metabolites (allelochemicals) below some critical level (Freeland and Janzen, 1974). However, since this is a per se mechanism and is species-specific, more investigations are required.

Although little information is known about the chemical properties of most grasses in the study sites, grasses accumulate relatively high levels of silica in their tissue which could be an alternative tactic, with potential benefits, including antiherbivore defense (Vicari and Bazely 1993; ElSayed et al. 2020; Quigley et al. 2020).

Graminivorous species differ in their dietary choices when feeding on graminoids (monocots) in natural grassland vegetation when compared to forbivorous or herbivorous species and this considered as species-specific (Joern, 1985). Bemays et al. (1989) have also reported that tannins are often considered a major class of allelochemical defense in dicotyledonous plant species (dicots) and they have also been considered as deterrents to graminivorous orthopteran species (Bemays and Chapman, 1977) which could partly explain the selection of grasses by graminivorous species.

Mandibular abrasion in both incisor and molar areas in graminivorous species (G) could be attributed to the fact that these species feed regularly on silica-rich grasses. These silica particles could act as a sand paper that wear the mandibles of these graminivorous species (ElSayed et al. 2020). It was reported that silica causes wear to insect mandibles which could potentially impact on the performance of herbivory (Baker et al., 1959; Vicari and Bazely, 1993; Massey and Hartley, 2009; ElSayed et al. 2020).

Our analysis of the gut contents of orthopteran species with mixed-feeding category (M) or even species of mixed feeding habit beside main category (i. e. Hm and Fm) could suggest that arthropod parts and other detritus of plant matters are not incidentally consumed but they are main part of their dietary preference. These species could intentionally feed on arthropod parts which were predominant in the gut of the entire dissected individuals. However, more detailed investigations and analyses on this aspect are required.

Conclusion

The gathered data on the comparatively small assemblage give only a hint concerning the whole story of evolution of functional food strategies among orthopeteran species. A general scheme for explicating the diet of a given orthopteran species, or other taxa group, could be started with detailed inspections of their mandibular morphological characteristics.

Although most species with forb feeding mandibles could feed on mixture of grasses and forbs, one of the confirmation avenue is associating mandibular characteristics with observations and data gathered from analyzing the gut contents.

It is hoped that more researchers will find that the study of morpho-mandibular characteristics and gut contents analysis is rewarding will contribute to the advancement of our knowledge concerning feeding strategies in Orthoptera. This research tries to open the door for more studies to analyze more mandibles from more taxa (Patterson, 1983).

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Conflict of interest

The authors declare no conflict of interest associated with this article and Prof. Dr. Ames Cheryl Lynn (International Integrative Research and Instruction Unit, Tohoku University, Japan) for her persistent cooperation and continuous encouragement.

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Διατροφική Κατηγοριοποίηση ορισμένων ειδών Caelifera και Ensifera (Insecta: Orthoptera) από επιλεγμένους αγρούς στην πόλη Sendai της Ιαπωνίας

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ΠΕΡΙΛΗΨΗ

Αν και τα είδη των ορθοπτέρων έχουν συχνά θεωρηθεί ως πολυφάγα φυτοφάγα, τα περισσότερα από αυτά παρουσιάζουν ποικίλους βαθμούς επιλεκτικότητας και ιδιαίτερες προτιμήσεις ενδιαιτήματος. Επιπλέον, ορισμένα είδη παρουσιάζουν ιδιόμορφες προτιμήσεις διατροφής που χρήζουν περαιτέρω διερεύνησης. Δείγματα από ένα σύνολο 43 ειδών ορθοπτέρων, από 7 οικογένειες, 12 υποοικογένειες και 13 φυλές, από πέντε αγρούς στην πόλη Σεντάι της Ιαπωνίας, συλλέχθηκαν για να διερευνηθούν οι διατροφικές τους προτιμήσεις, και ταξινομήθηκαν σε επτά κύριες διατροφικές κατηγορίες με βάση την εξέταση των μορφολογικών χαρακτηριστικών της γνάθου και αναλύσεις του μεταθανάτιου περιεχομένου του εντέρου.