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Autumn dietary overlaps among three sympatric mesocarnivores in the central part of Stara Planina Mountain, Bulgaria

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Abstract. Food habits and dietary overlaps of the three sympatric mesocarnivores (golden jackal *Canis aureus*, red fox *Vulpes vulpes*, and stone marten *Martes foina*) in a mountain-forest region in central Bulgaria were investigated. These species showed high dietary overlaps, commonly consuming rodents and fruits through studied period. Moreover, their dietary overlaps were higher in November than in the earlier months, because rodents were a predominant prey for all carnivore species in this season. Spatiotemporal separations of smaller carnivores from larger competitor may enable their sympatry, when their food habits were similar.

Key words: *Canis aureus*, generalist predator, *Martes foina*, trophic niche, *Vulpes vulpes*.

Interspecific competition among sympatric carnivores is a key for their population successes and the faunal structure (Palomares and Caro 1999; Linnell and Strand 2000). Larger carnivores often harass and, in many cases, replace smaller ones through direct confrontation and killing (Kamler et al. 2003, 2013), when their trophic niches are highly overlapped (Donadio and Buskirk 2006). Contrastingly, medium-sized carnivores (i.e., mesocarnivores defined as species with < 15 kg body mass; Roemer et al. 2009) are often generalist predators, and their trophic niches potentially overlap. According to the competitive exclusion theory (Hardin 1960), sympatric carnivores need to separate their trophic niches (Fedriani et al. 2000; Vanak and Gompfer 2009; Kamler et al. 2012; Tsunoda et al. 2017). Nevertheless, these species co-occur, sharing the same food sources within a habitat, where staple food sources are abundant (Linnell and Strand 2000; Carvalho and Gomes 2004; Lanszki et al. 2006).

The golden jackal (*Canis aureus*), the red fox (*Vulpes vulpes*), and the stone marten (*Martes foina*) widely distribute across the Balkan Peninsula (Popov and Sedefchev 2003). Their overall diets are potentially

overlapping, mainly consuming rodents, carrion, insects, and fruits in temperate regions in Europe (Zhou et al. 2011; Hayward et al. 2017; Soe et al. 2017), indicating that resource partitioning is needed for their successful sympatry. In central Bulgaria, we found trophic niche separations between jackals and the others in winter: jackals relied on carrions of domestic mammals or wild ungulates (Raichev et al. 2013), while foxes and martens mainly foraged rodents (Hisano et al. 2014; Tsunoda et al. 2017). However, we predict that their trophic niches might highly overlap when staple food sources are abundant, as observed in some previous researches (Carvalho and Gomes 2004; Lanszki et al. 2006, 2016; Barrull et al. 2014). To assess our prediction, we investigated food habits and dietary overlaps of the three mesocarnivores in autumn, when some food resources (e.g., rodents, fruits, and/or insects) might be more available than in winter, in a mountain forest region of central Bulgaria.

Materials and methods

The study area (approximately 8 km²; 42°36'–42°N, 25°25'–46°E) is located in the Central Stara Planina

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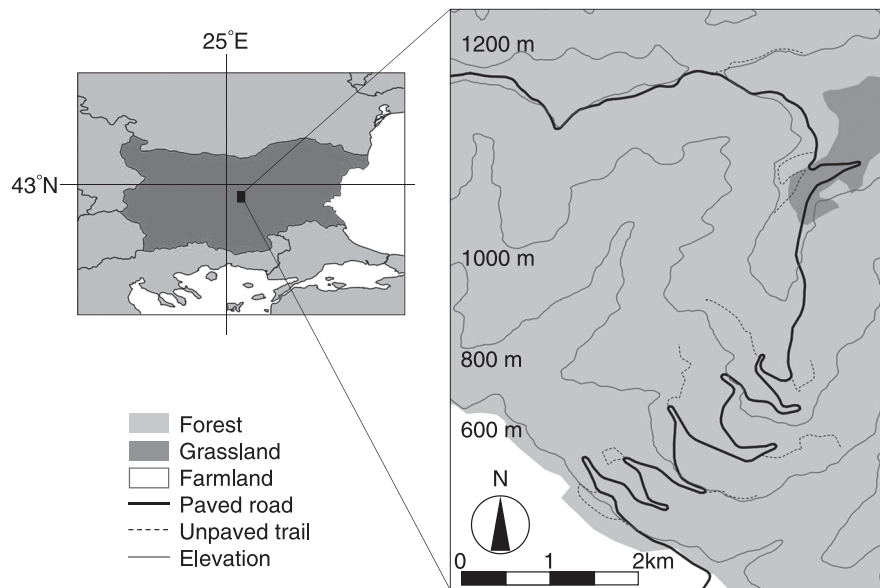


Fig. 1. Location of the study area and transect route.

Mountains, with an elevation of 500 m to 1300 m above sea level (a.s.l.), on the lower southern slopes of the eastern Balkan Mountains (Fig. 1). Average temperature and total precipitation during the sampled period ranged from 8°C to 23°C and from 42.9 mm to 76.2 mm, respectively, at the foothill of the study area (Shipka town, 650 m a.s.l.; data source from World Weather Online, <https://www.worldweatheronline.com/>, Accessed 5 October 2018). The area was entirely covered with secondary oak forests (*Quercus* sp.) in lower elevations (up to 1000 m a.s.l.) and with primarily beech forests (*Fagus sylvatica*) in higher elevations, while there were few settlements and agricultural lands.

We sampled the scats of the target carnivores across a primary paved-road and tributary unpaved-trails (total distance: approximately 8 km; Fig. 1) once a week from September to November in 2016. We searched the scats both sides of each transect. We identified interspecific differences of scats according to their diameters, shapes, textures, and odours in accordance with the protocol operated in our previous research (Hisano et al. 2016). Because the pine marten (*Martes martes*) occurred in higher elevations in the studied area (Popov and Sedefchev 2003), we sampled martens' scats only from an elevation below 1000 m a.s.l., where there was no evidence of pine marten presence (Raichev 2018). The sampled scats were collected in plastic bags, carried into the laboratory and then preserved at -20°C in a freezer.

The scat samples were washed through a sieve (0.5 mm

mesh) with water, sorted under a 10× magnifying lens, and identified contents with reference to collections of specimens from the study area, the Laboratory of Zoology, and Anatomy at Trakia University. We divided them into eight categories, excluding non-food (fallen leaf, sand, and gravel) and unidentified items: rodents, hare, carnivores (mainly domestic dogs), ungulates (mainly roe deer), birds, insects, fruits, and trash (envelops of salami and sausage). All food items were air-dried at room temperature for at least two weeks and then weighed (g) for each food category. For dietary analyses, we estimated the relative frequency of occurrence (RFO; %) and average values of the proportion of dry weight (PDW; %) for all food categories following equations:

$$\text{RFO (\%)} = \frac{\text{the number of occurrences of a food category}}{\text{the total number of all food categories}} \times 100$$

$$\text{PDW (\%)} = \frac{\text{dry weight of a food category in a scat}}{\text{total dry weight of all food items in the one scat}} \times 100.$$

For interspecific comparisons of dietary changes through the studied period, we analyzed monthly changes of the RFO or PDW of main food categories (observed > 10% for both RFO and PDW) in the carnivores' diets using generalized linear model (GLM). For explanatory variable, we used month or species (with dummy variable transformation; the values on martens or in September were defined as the baseline variable). We used the RFO

(binomial distribution, logit link function) and PDW (Gaussian distribution, identity link function) for response variable. When we found any statistical significances in monthly or interspecific differences, we then performed post hoc Tukey's test for multiple comparison for every month or species pair. These analyses were performed using R ver. 3.3.2 (R Core Team 2016) and the 'glht' function of 'multcomp' package (Hothorn et al. 2008) for Tukey's test.

We also examined interspecific or monthly differences in fruits consumptions among the studied carnivores. However, several fruit species, including the pieces of some unidentified species, were often mixed in the contents from a scat sample, and it was hard to distinguish their weights by each species correctly. Therefore, we recorded the number of occurrences of each fruit species from the sampled scats and then estimated the proportion of occurrences (PO; %) as in the following equation:

$$\text{PO (\%)} = \frac{\text{the total number of occurrences of a fruit species}}{\text{the total number of the scats sampled}} \times 100.$$

Finally, we calculated Pianka's index for dietary overlap between each carnivore-pair as in a following equation:

$$\text{Pianka's index} = \frac{\sum (p_{ji} \times p_{ki})}{(\sum p_{ji}^2 \times \sum p_{ki}^2)^{1/2}}$$

where p_{ji} and p_{ki} represent the RFO or PDW of a food category i occurred from the diets of carnivore species j and k , respectively (Pianka 1973). The index ranges from 0 (no overlap) to 1 (complete overlap). To determine the significance of dietary overlap, we performed a null-model test with 1000 randomizations, using the 'scrambled-zeros' randomization algorithm (Winemiller and Pianka 1990). The analysis was performed using the 'niche_null_model' function of 'EcoSimR' package (Gotelli et al. 2015) in R.

Results

We collected 39 scats from golden jackal, 95 scats from red fox, and 39 scats from stone marten. Rodents were the predominant food category, followed by fruits, in the diets of jackals and foxes (Table 1). Insects also occurred relatively often in the diets of the two canids, whereas their dry weights were in smaller proportions (Table 1). Fruits were the predominant food category, followed by rodents in the overall diets of stone martens (Table 1).

Table 1. The total number of occurrences (n), the relative frequency of occurrence (RFO) and the proportion of dry weight (PDW) for food categories in the diets of golden jackals, red foxes and stone martens through the studied period in central Bulgaria

Food category	Golden jackal ($N=39$)			Red fox ($N=95$)			Stone marten ($N=39$)		
	n	RFO	PDW	n	RFO	PDW	n	RFO	PDW
Rodents	30	40.0	50.2	72	40.9	48.9	24	41.4	19.3
Hare	2	2.7	2.4	1	0.6	0.0<	0	0.0	0.0
Carnivores	2	2.7	4.9	1	0.6	0.5	0	0.0	0.0
Ungulates	0	0.0	0.0	3	1.7	2.1	0	0.0	0.0
Birds	0	0.0	0.0	0	0.0	0.0	1	1.7	0.0<
Insects	14	18.7	0.2	30	17.0	0.2	3	5.2	0.2
Fruits	25	33.3	41.6	68	38.6	48.2	29	50.0	80.5
Trash	2	2.7	0.8	1	0.6	0.1	1	1.7	0.0<

N represents the total number of the sampled scats.

Other food categories were relatively lower proportions (< 5%) for both RFO and PDW in the diets of the three carnivores (Table 1).

Rodents increased from September (RFO = 29.2%; PDW = 43.1%) to October (RFO = 47.1%; PDW = 68.0%) and November (RFO = 44.1%; PDW = 64.8%) in jackal's diet, while fruits once decreased from September (RFO = 33.3%; PDW = 36.7%) to October (RFO = 23.5%; PDW = 22.0%) and then increased to November (RFO = 38.2%; PDW = 34.4%; Fig. 2); however, there were no statistical significances for monthly differences by GLM analyses (Appendix 1). In the diets of red foxes, rodents increased from September (RFO = 24.4%; PDW = 22.6%) to November (RFO = 50.0%; PDW = 65.5%), and these monthly differences were significant by both GLM analyses (Appendix 1) and post hoc Tukey's test ($P < 0.05$; Fig. 2). On the other hand, fruits in the fox diets gradually decreased (September, RFO = 41.5%, PDW = 72.9%; October, RFO = 37.5%, PDW = 40.5%; November, RFO = 37.5%, PDW = 30.5%); we found significant differences for the PDW by GLM analyses (Appendix 1), but not any differences by Tukey's test (Fig. 2). As well as in fox diets, rodents in the diets of stone martens increased from September (RFO = 29.6%; PDW = 7.2%) to November (RFO = 57.9%; PDW = 56.9%), while fruits decreased during the same period (September, RFO = 59.3%, PDW = 87.5%; November, RFO = 36.8%, PDW = 43.1%; Fig. 2). These monthly differences were statistically significant only in the PDW by Tukey's test (Fig. 2).

For interspecific comparisons within each month, we found no significant interspecific differences for the RFO

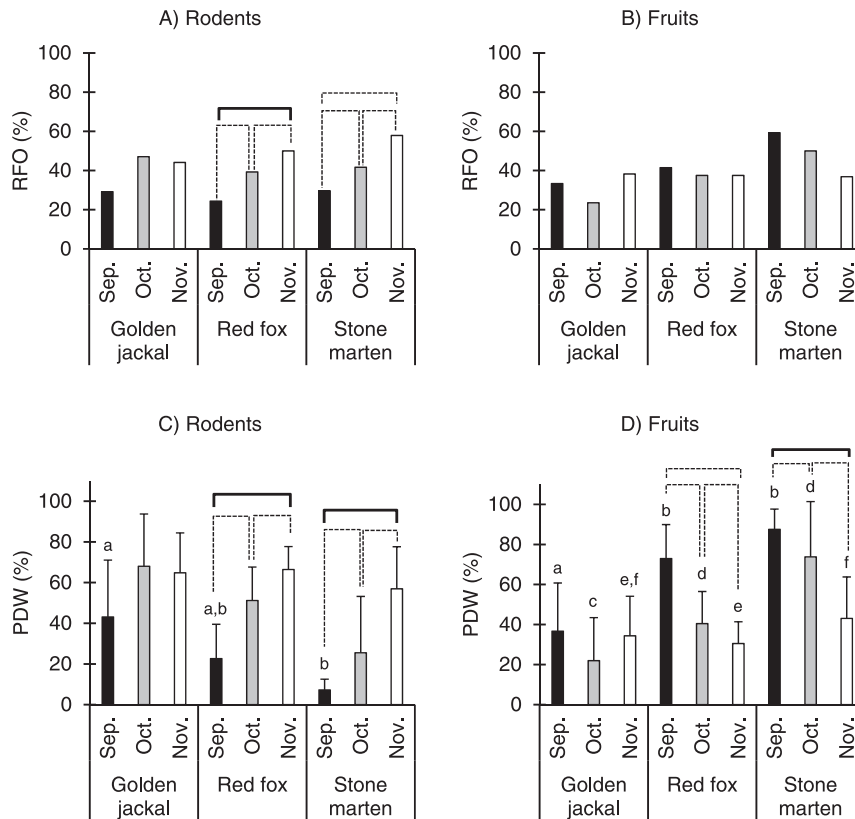


Fig. 2. Monthly changes in the relative frequency of occurrence (RFO) and the proportion of dry weight (PDW; the averages with 95% confidence intervals were represented) for rodents and fruits in the diets of golden jackals, red foxes, and stone martens in central Bulgaria. If there were any statistical significances by generalized linear model analyses, polylines and lowercase letters (i.e., a–f) were shown above bars for representing monthly and interspecific comparisons, respectively. Bold-solid polyline represents significant monthly-difference for each carnivore by the Tukey's multiple comparison test ($P < 0.05$), whereas thin-dotted lines represent non-significances. Different lowercase letters (e.g., a and b) represent statistical interspecific-differences in each month by Tukey's test ($P < 0.05$), whereas the same letters represent non-significances.

(Appendix 2). On the other hand, we found significantly differences for the PDW of rodents in the diets of between jackals and martens in September by GLM analysis (Appendix 2) and post hoc Tukey's test ($P = 0.049$; Fig. 2). Moreover, we also found significant differences on the PDW of fruits in the diets of the three carnivores by the GLM analyses (Appendix 2): fruits were more predominant foods for both martens and foxes in both September and October than for jackals (Tukey's test for PDW; $P < 0.001$ to $P = 0.023$), while there was significant difference between foxes and martens only in November ($P = 0.008$; Fig. 2).

Mulberry (*Morus nigra* and *M. alba*) and pear (*Pyrus communis*) were relatively predominant fruits in the diets of both jackals and foxes in September but gradually decreased in later months (Table 2). Cornelian cherry (*Cornus mas*), as well as mulberry in September, was the predominant fruits in the diets of martens in September and October but subsequently decreased in November

(Table 2). In November, the occurrence of dog rose (*Rosa canina*) increased and became the predominant fruit in the diets of the studied carnivores (Table 2).

Dietary overlaps among the three carnivores were relatively high: we found significant dietary overlaps through the study period, except for jackals–martens in October (0.55), assessed by null-model test (Table 3). Dietary overlap indices in each species pair tended to decrease from September to October and then increased to November (Table 3).

Discussion

We found that the sympatric golden jackals, red foxes, and stone martens commonly consumed rodents and fruits and showed high dietary overlaps. Although the three carnivores shared common food resources through the studied period, we observed that their diets slightly differentiated in September and October. Golden jackals

Table 2. Monthly changes in the proportion of occurrences (%) of fruits in the diets of golden jackals, red foxes and stone martens in central Bulgaria

Fruit species English name	Academic name	Golden jackal			Red fox			Stone marten		
		Sep.	Oct.	Nov.	Sep.	Oct.	Nov.	Sep.	Oct.	Nov.
Mulberry	<i>Morus nigra</i> and <i>M. alba</i>	36.4	20.0	11.1	65.0	25.0	2.1	36.8	14.3	7.7
Cornelian cherry	<i>Cornus mas</i>	27.3	10.0	5.6	10.0	28.6	8.5	57.9	71.4	23.1
Common hawthorn	<i>Crataegus monogyna</i>	0.0	0.0	11.1	5.0	0.0	2.1	0.0	0.0	7.7
Blackthorn	<i>Prunus spinosa</i>	0.0	0.0	0.0	5.0	3.6	2.1	0.0	0.0	0.0
Dog rose	<i>Rosa canina</i>	0.0	0.0	38.9	5.0	17.9	40.4	0.0	0.0	38.5
Pear	<i>Pyrus communis</i>	27.3	20.0	5.6	45.0	21.4	10.6	15.8	0.0	7.7
Plum	<i>Purunus domestica</i>	18.2	20.0	11.1	10.0	3.6	0.0	15.8	0.0	7.7
Grape	<i>Vitis</i> spp.	18.2	0.0	0.0	5.0	7.1	0.0	0.0	28.6	0.0
Number of the sampled canivore faeces in each month		11	10	18	20	28	47	19	7	13

Table 3. Pianka's indices for the dietary overlaps among golden jackals, red foxes and stone martens. The 95% ranges of simulated values by null-model test were showed in parentheses

Species-pair	Dietary index	September	October	November	Whole periods
Jackal-Fox	RFO	0.96** (0.10–0.84)	0.95*** (0.03–0.86)	0.99** (0.00–0.93)	0.99** (0.05–0.91)
	PDW	0.91** (0.00–0.82)	0.87* (0.00–0.87)	0.96* (0.00–0.95)	0.99** (0.01–0.99)
Fox-Martens	RFO	0.90** (0.01–0.88)	0.98** (0.02–0.95)	0.98* (0.00–0.92)	0.97** (0.03–0.95)
	PDW	0.97** (0.00–0.96)	0.88* (0.00–0.77)	0.97* (0.00–0.94)	0.85* (0.00–0.85)
Jackal-Martens	RFO	0.90** (0.05–0.85)	0.88* (0.00–0.88)	0.95* (0.00–0.93)	0.95** (0.04–0.92)
	PDW	0.80** (0.00–0.77)	0.55 (0.00–0.92)	0.99* (0.00–0.99)	0.80* (0.00–0.80)

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

mainly preyed on rodents in these months, while stone martens primarily consumed fruits. Red foxes were mainly frugivorous in September, and then increased rodents consumptions in October though they still relied more on fruits than jackals. Both golden jackals and red foxes preferred rodents when those preys were available (Lanszki et al. 2006; Lanszki and Heltai 2010). Larger carnivores, however, are generally more dominant in resource patches than smaller ones (Palomares and Caro 1999; Linnell and Strand 2000): thus, foxes might partition food resources by increasing fruits consumptions, to avoid competitions with jackals. Red foxes potentially suppress or kill sympatric martens, maybe becoming the dominant competitor (Serafini and Lovari 1993; Lindstrom et al. 1995; Barrull et al. 2014), and thus there is a need for resource partitioning for their sympatry. Although their overall diets were highly overlapped for category basis (Table 3), we found that the consumed fruits were different between martens and the two canids: both canids might consume ripe fallen fruits (e.g., mulberry and pear) on the ground, while martens could consume arboreal mulberry and/or cornelian cherry (Table 2),

owing to their smaller body size and tree-climbing behavior (Serafini and Lovari 1993). Previous researches also indicated that arboreal fruits consumptions by stone martens contributed to spatial segregations from red foxes at finer scale and partitioning dietary niches (Serafini and Lovari 1993; Padial et al. 2002). The differentiations in fruits consumptions might contribute to partition their foraging site used and thus decrease their direct confrontations. Moreover, we suppose that the tree-climbing behavior was also advantageous for martens to escape from aggressions or harassments by the two canids.

In November, fruits in the diets of both foxes and martens decreased with increasing rodents, probably due to the end of fruiting season and less availability of some species (e.g., mulberry, cornelian cherry, and pear). Moreover, we also observed that the three carnivores consumed fruits of dog rose more frequently in this month (Table 2). We suppose that declines of available fruits in November led to the increase of higher dietary overlaps among the three carnivores. The dietary overlaps among sympatric carnivores can increase direct competitions on resource patches (Palomares and Caro 1999;

Linnell and Strand 2000), provoking their spatiotemporal segregations (Fedriani et al. 2000; Kamler et al. 2012; Barrull et al. 2014). Previous researches demonstrated that both red foxes and stone martens were segregated from golden jackals for space or time (Shamoon et al. 2017; Tsunoda et al. 2018), possibly reducing their direct encounters on resource patches.

In conclusion, we observed higher dietary overlaps among sympatric golden jackals, red foxes, and stone martens in autumn, comparing to our previous observations in winter (Raichev et al. 2013; Hisano et al. 2014; Tsunoda et al. 2017). Despite relatively small sample sizes for both jackals and martens, our observations on their diets were consistent with previous researches conducted in other European regions (Serafini and Lovari 1993; Carvalho and Gomes 2004; Lanszki et al. 2006, 2016; Padial et al. 2002; Barrull et al. 2014). Although the present study showed that the studied carnivores shared common food resources (i.e., fruits and rodents), we supposed that differentiations in foraging patterns for fruits (Table 3) as well as spatiotemporal separations (Tsunoda et al. 2018) might enable them to coexist within a habitat. Our findings indicated that competitive interactions among sympatric carnivores might be changeable seasonally and ecological or behavioral responses to dominant competitors might differ among species.

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Appendix 1.

The estimated coefficient and standard error for the results of generalized linear model analyses for monthly comparison in each species

Food	Species	RFO			PDW		
		(Intercept)	October	November	(Intercept)	October	November
Rodents	Jackal	0.56 ± 0.63	0.83 ± 1.01	1.05 ± 0.89	-2.92 ± 0.79***	0.97 ± 1.15	1.34 ± 1.01
	Fox	0.00 ± 0.45	1.30 ± 6.42*	1.74 ± 6.07***	-2.16 ± 0.35***	1.30 ± 6.42	1.23 ± 0.42**
	Marten	-0.32 ± 0.47	1.24 ± 0.95	2.02 ± 0.90*	-1.40 ± 0.22***	0.56 ± 0.43	0.87 ± 0.35*
Fruits	Jackal	0.98 ± 0.68	-1.39 ± 0.94	-0.03 ± 0.86	-2.57 ± 0.55***	-0.91 ± 0.80	1.06 ± 0.70
	Fox	1.74 ± 0.64**	-0.64 ± 0.76	-1.17 ± 0.70	-0.76 ± 0.34*	-0.87 ± 0.44*	-0.92 ± 0.40*
	Marten	1.67 ± 0.63**	-0.12 ± 1.25	-1.52 ± 0.84	-0.10 ± 0.07**	-0.30 ± 0.14*	-0.36 ± 0.12**

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Appendix 2.

The estimated coefficient and standard error for the results of generalized linear model analyses for interspecific comparison in each month

Food	Month	RFO			PDW		
		(Intercept)	Jackal	Fox	(Intercept)	Jackal	Fox
Rodents	Sep.	-0.31 ± 0.47	0.88 ± 0.78	0.32 ± 0.65	-1.40 ± 0.39***	-1.53 ± 0.65*	-0.76 ± 0.55
	Oct.	0.92 ± 0.84	0.47 ± 1.15	0.38 ± 0.96	-1.96 ± 0.84*	0.00 ± 1.09	0.07 ± 0.93
	Nov.	1.71 ± 0.77	-0.10 ± 1.00	0.04 ± 0.87	-0.53 ± 0.41	-1.05 ± 0.54	-0.35 ± 0.46
Fruits	Sep.	1.67 ± 0.63**	-0.69 ± 0.92	0.06 ± 0.89	-0.10 ± 0.24	-2.46 ± 0.39***	-0.65 ± 0.33
	Oct.	1.79 ± 1.08**	-2.20 ± 1.26	-0.69 ± 1.17	-0.40 ± 0.72	-3.07 ± 0.94**	-1.22 ± 0.81
	Nov.	0.15 ± 0.56**	0.80 ± 0.77	0.41 ± 0.63	-0.46 ± 0.36	-1.04 ± 0.47*	-1.21 ± 0.41**

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$