Zoomorphology (2014) 133:435–443
DOI 10.1007/s00435-014-0238-3

ORIGINAL PAPER

Seasonal plasticity of duodenal morphology and histology in *Passer montanus*

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Received: 28 April 2014 / Revised: 17 July 2014 / Accepted: 22 July 2014 / Published online: 13 August 2014

Abstract When facing seasonal environmental changes, flying birds and small mammals may develop adaptive gastrointestinal changes to optimize their digestive and absorptive strategies to meet the changing of physiologic needs. As a main component of gastrointestinal tract, small intestine is extraordinarily sensitive to food abundance, food quality, and other environmental factors. However, the detailed morphological adaptations of the small intestine during seasonal changes are largely unknown. Here, we studied the morphological and histological dynamics of duodenum from *Passer montanus* in Zhalong Nature Reserve in China during seasonal changes. The luminal and wall cross-section area were greater in spring and autumn than that in summer. Villus height and width went up to peak values in winter and showed similar seasonal dynamic changes with that of mucosal thickness, while villus atrophy accompanied by the deepest crypt depth was easily detected in summer. Epithelium thickness was coincident with villus atrophy except a sharp increase in summer. Submucosal thickness was negatively correlated with that of mucosa, while the size, but not total number, of duodenal glands was altered to reflect to seasonal changes. Neither the inner circular nor the outer longitudinal muscle showed seasonal morphological changes, indicating the relatively stable plasticity of intestine muscle structures. Taken together, we propose that phenotypic flexibility in digestive morphology and histology enables small birds to cope with remarkable seasonal changes.

Keywords Duodenum · Morphology · Histology · Dynamic changes · Adaptation

Introduction

The gastrointestinal tract is a long continuous tube extending from the top of stomach to the anus, which digests food mechanically and chemically, performs the processes of absorption, and eliminates the unabsorbed residue (Weaver 1997; Mendes et al. 2009). When facing spatiotemporal changes in environmental conditions, phenotypic flexibility of digestive physiology and other physiologic changes are necessary for an animal to maximize the energy release from ingested food and balance the energy needs for reproduction or other physiologic processes (Piersma and Dren 2003; del Valle et al. 2004; Cavieres and Sabat 2008; McWhorter et al. 2009; Brzek et al. 2011; Khalilieh et al. 2012). For optimal digestion and absorption as well as energy balance, the gastrointestinal tract of birds and small mammals can be modulated by changing its size, morphological features, enzyme activities, transport mechanisms, and other physiologic variables (Piersma et al. 1999; Karasov and McWilliams 2005; Sabat and Bozinovic 2008; McWhorter et al. 2009;

Communicated by Andreas Schmidt-Rhaesa.

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Sailer and Fietz 2009; Karasov 2011). As a main component of the gastrointestinal tract, the small intestine is extraordinarily sensitive to food abundance, food quality, dietary habitat, and other environmental factors, especially for winter-active small mammals and birds inhabiting cold regions or seasonally variable environments (Vogt and Lynch 1982; Bozinovic et al. 1990; del Valle and Lopez Mananes 2008; Karasov et al. 2011).

Several studies in flying birds and small mammals have demonstrated the morphological changes to the small intestine and other gastrointestinal tissues in response to energy requirements and environmental changes (Piersma et al. 1999; Karasov and McWilliams 2005; Brzek et al. 2009, 2011; Karasov 2011). The size of digestive organs has been shown to be modulated by food quality, food abundance, pregnancy, lactation, and other physiologic and environmental conditions (Hammond and Wunder 1991; del Valle et al. 2004; Sailer and Fietz 2009). For example, Killpack and Karasov (2012) found that wet mass of the intestine was significantly reduced in food-restricted house sparrows (*Passer domesticus*) compared with that of controls. Our recent paper also reported that the dry mass of both small intestine and large intestine of tree sparrows (*Passer montanus*) was significantly higher in autumn than that in winter, spring, or summer (Zheng et al. 2008). Although the morphological changes of gastrointestinal tract of small mammals and birds have been well studied (Hammond and Wunder 1991; Hammond and Kristan 2000; del Valle et al. 2004, 2006; del Valle and Lopez Mananes 2008; Zhang et al. 2009), the previous studies mainly focused on changes of intestinal length and mass—longer intestine means larger digestive volume and food capacity, and larger fresh and/or dry mass indicates more complicated microstructure of its digestive system and thus more efficient digestion and absorption (Sabat et al. 1998; del Valle et al. 2004; Sassi et al. 2007; Lavin et al. 2008). Seasonal changes of the more specific histological features of small intestine, which are critical for winter survival, reproduction, and other physiologic needs, require more thorough investigations.

The detailed structure of a specific digestive tube is associated with its special functions and has different sensitivities to the environment they lived in and energy requirement for different physiologic needs (Klasing 1999; Samanya and Yamauchi 2002; Vente-Spreeuwenberg et al. 2004; Lavin et al. 2008; Karasov 2011). Few studies have been performed to examine changes of the microstructure and functionality of the intestine. For example, Dou et al. (2001) reported that fasting causes rat intestinal atrophy with reduction in villus height, crypt depth, epithelial turnover, and migration. Samanya and Yamauchi (2002) reported that feeding dietary *Bacillus subtilis natto* depresses ammonia production and thus activates cell mitosis, leading to the increase of villus height of chicken small intestine. However, the detailed intestinal histological dynamics/changes, which are more informative for the digestive strategy and seasonal adaptation of small mammals and birds, remain largely unknown.

To precisely clarify the morphological adaptation of digestive tract, seasonal dynamics of duodenal histomorphology of *P. montanus* from a cold-temperate climate in northeastern China was systematically studied. The morphological and histological dynamics of duodenum fit well with environmental variation and different physiologic needs of *P. montanus* during season changes.

Materials and methods

Study area and animal collection

This study was carried out from Jun 2006 to Nov 2008 in Zhalong National Nature Reserve, Heilongjiang Province, China (46°48′–47°31.5′N, 123°51.5′–124°37.5′E). Zhalong is a permanent alkalescent freshwater swamp area overflowed by Wuyuer River and consists primarily of small man-made lakes, extensive meadows, and grasslands with a total area of 210,000 ha. The reserve is characterized by a north-temperate monsoon climate, where the average monthly temperature is maximal in July (22.8 °C) and lowest in January (−25.7 °C). The annual fluctuation of ambient temperature is great, with the lowest recorded temperature being −39.5 °C in January and the highest being 39.9 °C in July. The mean temperatures of winter (December–February), spring (March–May), summer (June–August), and autumn (September–November) are −14.7, 6.0, 17.0, and 6.8 °C, respectively. Annual rainfall here ranges between 400 and 550 mm with the maximum precipitation occurring in summer (Zheng et al. 2008). The study area belongs to the typical wetland ecological system dominated by species of annual or biennial herbs and shrubs (e.g., Compositate, Gramineae, Fabaceae, Cyperaceae, Rosaceae, and Polygonaceaed) with patched plantation of *Populus girinensis* and *Salix babylonica* surrounding the central reserve zone. This area harbors more than 260 bird species, and large quantities of insects, fishes, and mammals.

Tree sparrows (*P. montanus*), a small granivorous passerine inhibiting vast areas of the continents of Europe and Asia, were used in the present work. *P. montanus* is one of the dominant species in the studying area, which feeds mainly on weed seeds and grain crops throughout the year, while fresh stems and leaves, insects, and other foods of animal origin composite >30 % of their food intake during months from May to October, whereas *P. montanus* here are confronted with the interacting problems of food supplies during the winter months since snowfalls and shortened photoperiods restrict their foraging opportunities. *P. montanus* here breed twice yearly, since late May till early August. Nestlings are mainly fed with animal food, such as larval and adult insects, pupae, and spiders. In the present study, adult *P. montanus* were live-trapped monthly by mist net in the transition zone of Zhalong Reserve and carried to the laboratory where they were individually housed in cages under natural photoperiod and temperature. Food and water were supplied ad libitum. Sparrows with body mass of 17–20 g were used, while the sex was ignored in this study. This research was done under permit of the Zhalong National Nature Reserve. The use and care of animals were approved and directed by the Institutional Animal Care and Use Committee of Qiqihar University.

Histological structure of duodenum

The day after capture, animals were killed by decapitation. After necropsy, the gastrointestinal tract was excised and trimmed of mesenteries and fat. About 1-cm intestine was cut from the intermediate piece of duodenum and externally rinsed in physiologic saline and then slightly dried with tissue paper. The intestine tissue was fixed with 10 % formaldehyde solution, dehydrated in ascending series of ethanol, cleared in xylene, embedded in paraffin, sectioned, and stained with hematoxylin and eosin. The sections were observed with a Laser Scanning Confocal Microscope (LSM510, Zeiss). Total cross-section area (Section area), lumen area (cross-section area of the bore tube), wall area (section area minus lumen area), wall thickness (the difference of outer and inner radius of the cross section), mucosal thickness, submucosa thickness, inner circular muscle and outer longitudinal muscle thickness, villus height (the distance from the tip to the bottom of the villi) and width, crypt depths (the distance between the mouth of the crept and its base), epithelium thickness, duodenal gland density (the number of duodenal glands included in a defined area) and its cross-section area were measured (Pelicano et al. 2005) with Zeiss LSM Image Browser (Version 3.0).

Statistical analysis

Data collected from monthly (the second or third weekends per month) trapped animals were divided into four seasons: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). Statistical analyses were performed using SPSS (Statistical Package for the Social Sciences) 12.0. Seasonal differences of duodenum histological structures were analyzed by one-way ANOVA and LSD multiple comparisons, or Kolmogorov–Smirnov Test as indicated. Differences were considered statistically significant if $P < 0.05$. The correlation between mucosal layer and submucous layer, villus height and crypt depth, villus height and width was analyzed with bivariate correlate analysis.

Results

Duodenal morphology

The section area, lumen area, wall area, and wall thickness were measured to evaluate morphological seasonal changes of duodenum. Wall thickness of duodenum did not show a significant seasonal effect ($F_{(3,28)} = 0.585$, $P > 0.05$), whereas other variables did vary seasonally (Table 1). Both section area and wall area were greatest in spring and autumn, with the lowest values occurring in summer ($F_{(3,28)} = 9.098$, $P < 0.001$; $F_{(3,28)} = 6.731$, $P < 0.001$, respectively). The lumen area showed highest values in autumn, decreased in winter and spring, and the lowest values were found in summer ($F_{(3,28)} = 8.023$, $P < 0.001$).

Duodenal histology

Representative micrographs of the duodenum from sparrows collected in each season are shown in Fig. 1, and all the statistics of histological indexes are listed in Table 2. Thickness of mucosal layer was highest in winter, followed by spring and summer, and lowest in autumn ($F_{(3,28)} = 5.438$, $P < 0.01$). The highest values of villus height and width were registered in winter, followed by spring and autumn, while the lowest values were found in summer ($F_{(3,28)} = 7.821$, $P < 0.001$; $F_{(3,28)} = 9.329$, $P < 0.001$, respectively). Crypt depth also showed seasonal variations, being greater in summer than that during other parts of the year, among which, crypt depth in spring was greater than that in autumn and winter ($F_{(3,28)} = 14.878$, $P < 0.001$). Epithelium thickness showed significant seasonal changes as well, while winter values were higher than that in summer, followed by spring and autumn ($F_{(3,28)} = 8.756$, $P < 0.001$). Thickness of submucous layer exhibited highest values in summer and autumn, and lowest values in winter ($F_{(3,28)} = 10.914$, $P < 0.001$). Thickness of inner circular ($F_{(3,28)} = 0.646$, $P > 0.05$) and outer longitudinal muscle ($F_{(3,28)} = 1.249$, $P > 0.05$) showed no significant seasonal differences, although the outer longitudinal muscle was relatively thicker in winter and spring.

Villus height and width decreased in proportion from winter to autumn with a coefficient of 0.706 (Fig. 2; $P < 0.001$). However, the villus height was negatively correlated with crypt depth during the seasonal variations

Table 1 Seasonal changes of duodenal section

	Winter (*n* = 7)	Spring (*n* = 10)	Summer (*n* = 10)	Autumn (*n* = 5)
Section area (mm^2)	4.18 ± 0.96^{A,B}	5.01 ± 0.31^{A}	3.81 ± 0.55^{B}	5.13 ± 0.48^{A}
Lumen area (mm^2)	0.285 ± 0.124^{A,B}	0.369 ± 0.102^{A}	0.201 ± 0.098^{B}	0.527 ± 0.211^{C}
Wall area (mm^2)	3.90 ± 0.84^{A,B}	4.64 ± 0.72^{A}	3.61 ± 0.56^{B}	4.60 ± 0.41^{A}
Wall thickness (μm)	838.1 ± 28.35	889.6 ± 25.61	851.3 ± 22.06	846.6 ± 69.09

n number of individuals

All data are presented as mean ± SEM. Different letters indicate significant differences between seasons (ANOVA)

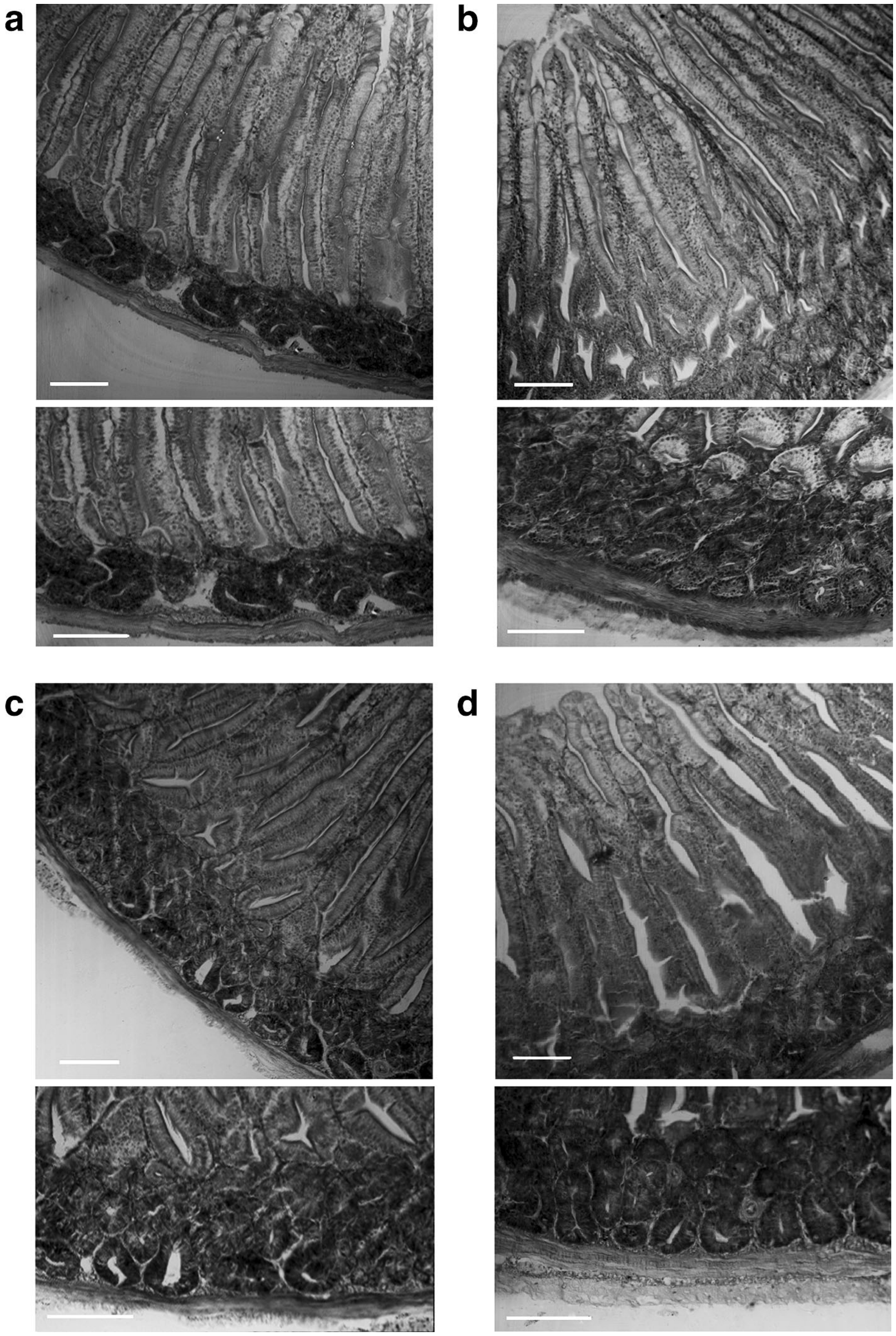

Fig. 1 Representative photomicrographs of duodenal sections of *Passer montanus* in winter (February, **a**), spring (May, **b**), summer (July, **c**) and autumn (November, **d**). *Scale bars* 100 μm

Table 2 Seasonal changes of duodenal histomorphology (μm)

	Winter ($n = 7$)	Spring ($n = 10$)	Summer ($n = 10$)	Autumn ($n = 5$)
McL thickness	744.0 ± 23.45^{A}	655.3 ± 35.53^{B}	$605.4 \pm 13.42^{B,C}$	571.9 ± 45.38^{C}
Villus height	711.9 ± 28.52^{A}	572.6 ± 39.48^{B}	496.7 ± 10.14^{C}	$557.3 \pm 46.58^{B,C}$
Villus width	71.56 ± 2.305^{A}	55.95 ± 1.442^{B}	53.77 ± 4.425^{B}	54.82 ± 6.444^{B}
IC depth	55.95 ± 4.666^{A}	131.87 ± 17.982^{B}	164.20 ± 9.094^{C}	75.51 ± 6.734^{A}
Epithelium thickness	29.73 ± 1.466^{A}	$24.61 \pm .0.767^{B}$	$27.33 \pm 1.319^{A,B}$	19.38 ± 1.873^{C}
SL thickness	102.82 ± 3.076^{A}	123.81 ± 11.123^{A}	166.78 ± 9.572^{B}	154.15 ± 2.605^{B}
ICM thickness	$21.90 \pm 1.992^{A,B}$	$22.07 \pm 2.276^{A,B}$	20.01 ± 1.327^{A}	24.46 ± 0.693^{B}
OLM thickness	13.74 ± 0.779	12.81 ± 1.477	11.74 ± 1.361	10.26 ± 0.364

IC intestinal crypt, *McL* mucosal layer, *SL* submucous layer, *ICM* inner circular muscle, *OLM* outer longitudinal muscle, *n* number of individuals

All data are presented as mean ± SEM. Different letters indicate significant differences between seasons

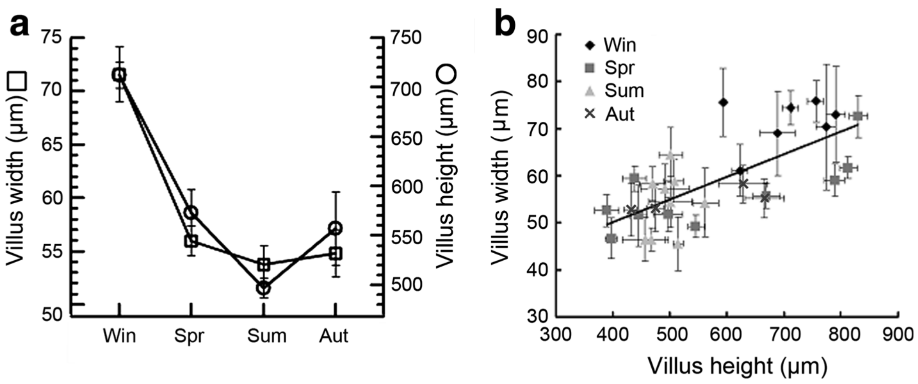

Fig. 2 Seasonal dynamics of the duodenal villus of *Passer montanus* in different seasons. **a** Villus width and height of *Passer montanus* in different seasons. **b** Correlation of villus width and height during seasonal changes. *Win* winter ($n = 7$); *Spr* spring ($n = 10$); *Sum* summer ($n = 10$); *Aut* autumn ($n = 5$). All data are presented as mean ± SEM

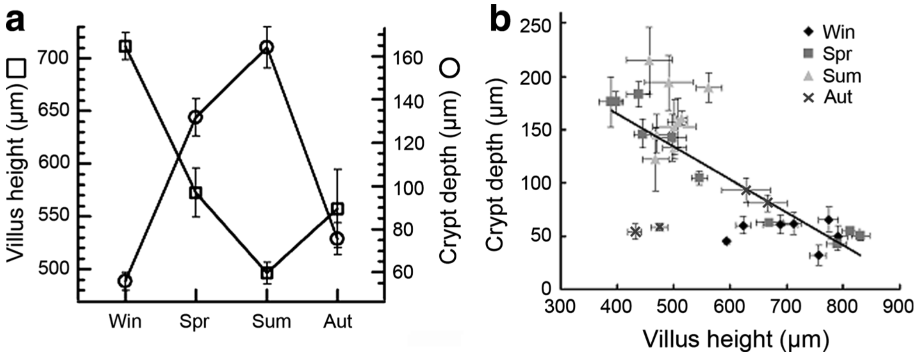

Fig. 3 Seasonal dynamics of villus height and crypt depth of *Passer montanus* duodenum. **a** Villus height and crypt depth of *Passer montanus* in different seasons. **b** Correlation of villus height and crypt depth during seasonal changes. *Win* winter ($n = 7$); *Spr* spring ($n = 10$); *Sum* summer ($n = 10$); *Aut* autumn ($n = 5$). All data are presented as mean ± SEM

(Fig. 3; $r = -0.744$, $P < 0.001$). In addition, the thickness of mucosal layer was negatively correlated with that of submucous layer, with a coefficient of -0.726 (Fig. 4; $P < 0.001$).

Section area of single duodenal glands in the four seasons significantly increased over summer and autumn, which was characterized by the right shifted accumulative frequency traces in those two seasons ($P < 0.001$). In contrast, the gland density decreased significantly in summer and autumn (Fig. 5b, $P < 0.05$).

Discussion

Duodenal morphology

Since duodenum is one of the main sites for digestion and absorption, its morphological and histological characterizations reflect differences in energy requirement and digestive strategy (Bozinovic et al. 1990; Dou et al. 2001; del Valle and Lopez Mananes 2008). There are two possible adaptive morphology changes of digestive tract in

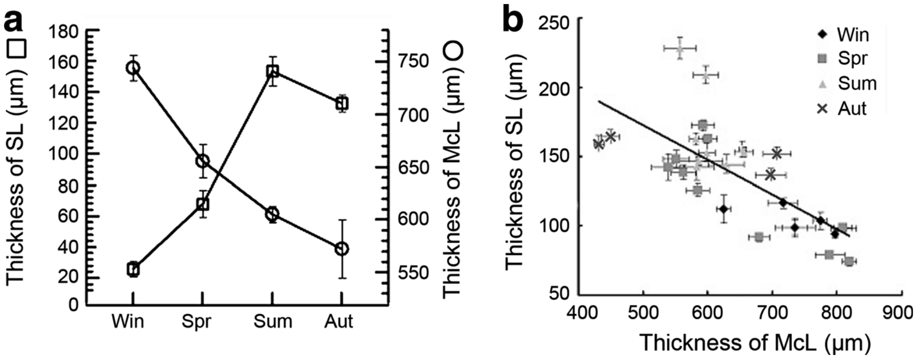

Fig. 4 Seasonal dynamics of mucosal layer and submucous layer of *Passer montanus* duodenum. **a** Thickness of mucosal layer and submucous layer of *Passer montanus* in different seasons. **b** Correlation of mucosal layer thickness and that of submucous layer during seasonal changes. *Win* winter ($n = 7$); *Spr* spring ($n = 10$); *Sum* summer ($n = 10$); *Aut* autumn ($n = 5$); *McL* mucosal layer; *SL* submucous layer. All data are presented as mean ± SEM

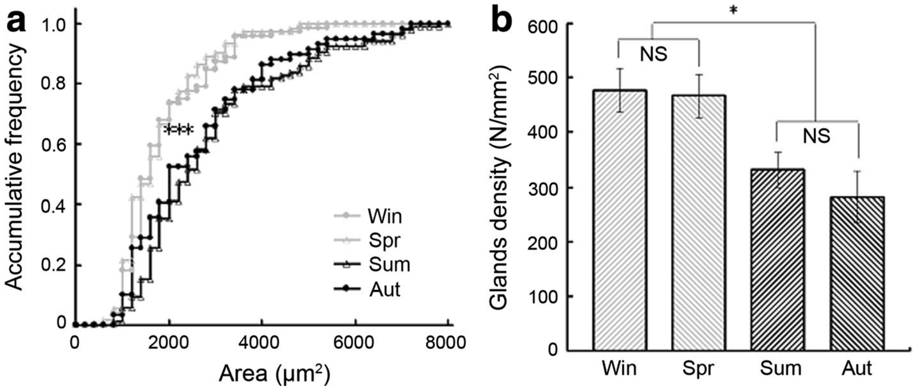

Fig. 5 Seasonal changes of gland section area and gland density of *Passer montanus* duodenum. **a** Accumulative frequency of duodenal gland section area in different seasons. *Win* winter ($n = 60$ glands from seven sparrows); *Spr* spring ($n = 71$ glands from ten sparrows); *Sum* summer ($n = 111$ glands from ten sparrows); *Aut* autumn ($n = 105$ glands from five sparrows). (Kolmogorov–Smirnov test, $***P < 0.001$). **b** Duodenal gland density of *Passer montanus* in different seasons. *Win* winter ($n = 7$); *Spr* spring ($n = 10$); *Sum* summer ($n = 10$); *Aut* autumn ($n = 5$). Data are presented as mean ± SEM. (ANOVA, $*P < 0.05$)

small mammals and birds: (1) the digestive capacity represented by the length and section area of digestive tract or (2) the histological changes of digestive tracts, such as the microvillus and digestive gland, which may lead to changes in digestion and absorption efficiency (Sabat et al. 1998; del Valle et al. 2004; Sassi et al. 2007; Cavieres and Sabat 2008). Our previous studies found that the mean body mass of *P. montanus* in this study area maintained between 18 and 19 g and showed little seasonal variation (Zheng et al. 2008). The mass of small intestine showed significant seasonal dynamics, being greatest in autumn and declining to its lowest value in spring (Zheng et al. 2008). Here, we mainly focused on the dynamics of duodenal tissue structures during the seasonal changes. The larger luminal area in spring and autumn increases the total capacity for breakdown and absorption of nutrient, allowing the greater food consumption of birds during these seasons (Klasing 1999; Karasov and McWilliams 2005; Zhao and Wang 2007; McWhorter et al. 2009). The larger wall area could be due to several possibilities, such as the increase of muscle thickness, gland size, villus height, or other duodenal structures (Weaver 1997; Karasov and McWilliams 2005). In the present work, we found that mucosal layer and villus height correlated with the larger duodenal wall area in autumn, winter, and spring, whereas the deeper crypt and thicker submucosa were accompanied with the duodenal wall atrophy in summer (Tables 1, 2). Thus, to balance the great energy expenditure of reproduction in summer when the available food with higher quality is abundant, investment on digestions tends to be cut back, evidenced by the decreased section area, wall area, and lumen area (Piersma and Dren 2003; Caviedes-Vidal et al. 2007; Sailer and Fietz 2009; Zhang et al. 2009).

Duodenal histology

The length and mass of each digestive organ were previously used as main indexes to study their seasonal dynamics, lacking attention to the fine details (Sabat et al. 1998; Piersma and Dren 2003; Sassi et al. 2007; Lavin et al. 2008). Histological measurements of the duodenum of *P. montanus* in northeast China were performed here to precisely study the seasonal dynamics and adaptive changes of digestive tract.

Mucosal layer, the innermost layer consisting of epithelial lining, lamina propria, and muscularis mucosae (Klasing 1999; Dou et al. 2001; Samanya and Yamauchi 2002), correlated well with section area. The section and luminal area decreased from autumn to winter, while the thickest mucosal layer was presented in winter when the available food is in lower quality (Zheng et al. 2008; Khalilieh et al. 2012). In spring when the gradually increased food abundance allows the lower investment on absorption, section, and luminal area increased gradually but was accompanied with the decreased mucosal thickness. The sharp decline of the section area and the mucosal thickness in summer fits well with physiologic needs of sparrows for reproduction (McWhorter et al. 2009; Zhang et al. 2009), whereas the section and luminal area increased gradually in autumn, restored intestinal capacitance for the increased food intake (del Valle et al. 2004; Karasov et al. 2004; Sassi et al. 2007).

Strikingly, the thickness of mucosa was negatively correlated with that of submucosal layer with a coefficient of −0.726 (Fig. 4). The thickest submucosa in summer and autumn would strengthen the self-protection of duodenum and may increase digestive and absorptive efficiencies, while the highest food abundance and food quality allow the gradual reduction in villus size to save energy. But in winter when food is in lower quality, the thickest mucosa is essential for sparrows to get the maximum digestion and absorption efficiencies, while the relatively thinner submucosa is sufficient to support local absorptions.

Villus height and width showed similar seasonal dynamics. They both decreased from winter to summer, while villus atrophy was clearly observed in summer but turned up in autumn (Fig. 2). Interestingly, crypt depth showed exactly opposite extremes to that of villus height and width (Figs. 2, 3). Considering that food abundance and food quality are reported to modulate villus morphology (Weaver 1997; Baurhoo et al. 2007) and that the deeper crypt depth is associated with the higher food quality (Vente-Spreeuwenberg et al. 2004), the villus atrophy accompanied with the deepest crypt depth in summer was unlikely caused by the decrease of cell renewal, but the increased rate of cell loss (Hall and Byrne 1989; Pluske et al. 1997; Samanya and Yamauchi 2002; Tako et al. 2004; Abd El-Khalek et al. 2011). The dynamics of epithelium thickness was coincident with that of villus atrophy except a sharp increase in summer. Since defect in intestinal enterocyte proliferation leads to the reduction of epithelium thickness (Rempel et al. 2000), the larger epithelium thickness in summer is probably contributed by the newly derived cells from the crypt.

As one of the main components of submucosa, duodenal glands secret mucus-rich alkaline material to protect duodenum and provide favorable conditions for intestinal enzymes (Knott et al. 2004; Macea et al. 2006; Mendes et al. 2009). The volume of single duodenal glands was maximal in summer and autumn with its density reduced, and interestingly, the total area of submucosa changed at a rate proportionate to that of single glands during the seasonal changes (estimated from morphological data). Thus, the smaller gland density is most likely due to the larger volume of single duodenal glands. Duodenal glands also produce epidermal growth factor to stimulate intestinal epithelium proliferation (Farkas and Gero 1989; Schumacher and Krause 1995; Macea et al. 2006). Thus, the larger size of duodenal glands in summer and autumn may contribute to the renewal and the regeneration of duodenal mucosa when the increased food intake brings more mechanical damages to the innermost layer of the duodenum.

Muscularis contains spirally oriented smooth muscle cells arranged into two sublayers, the internal circular-orientated and the external longitude-orientated sublayers (Henry et al. 1998; Casotti et al. 2007). The inner circular and outer longitudinal muscle of *P. montanus* here showed little morphological changes among the four seasons, indicating the relatively stable muscle structure during seasonal acclimatization.

Taken together, we presented rarely studied but very important seasonal variation in gastrointestinal tract in wild population that can be critical for winter survival, reproduction, and other physiologic demands. The duodenal histomorphology of *P. montanus* in northeast China showed clearly, but very complicated seasonal variations, and the dynamics fits well with their different physiologic requirements and the environmental changes among the four seasons. For a better understanding of the digestive strategy of small birds, it will be nice to examine the effect of reproductive status and ontogeny on similar measures within these and other birds.

Acknowledgments We thank Drs. Cong Guo (Sichuan University, China) and Jinsong Liu (Wenzhou University, China) for comments on this manuscript. This work was supported by the National Basic Research of China (2007CB109106), the Scientific Research Fund of Heilongjiang Provincial Education Department (11531425, 12531750 and 12531764), the Natural Science Foundation of Heilongjian Province of China (C200624 and C201453), and the Program for Young Teachers Scientific Research in Qiqihar University (2010K-Z10).

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