

Food availability influences postmetamorphic growth in two spadefoot toad species (genus *Pelobates*)

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Abstract. Understanding how major life history traits such as body size and mass and growth change in response to resource availability is crucial in explaining life history trade-offs. We conducted a laboratory experiment with three (high, medium and low) feeding intensity treatments using metamorphs of two spadefoot toads species, *Pelobates syriacus* and *P. fuscus*, from syntopic populations. We tested how total food consumption, final body size and mass, body mass increase, body mass and length growth rates and growth efficiency are influenced by food availability. The responses to food availability differed significantly between the species with respect to the total food consumption, body mass increase, body mass growth rate and growth efficiency (i.e. the ratio between total amount of food consumed during the experiment divided by the increase in body mass). *P. syriacus* metamorphs had higher growth rates and growth efficiency than *P. fuscus* juveniles. Also, *P. syriacus* juveniles responded to differences in food level by increasing growth efficiency with decreasing food levels. Overall *P. syriacus* seems better adapted to shortages in food availability than *P. fuscus*. Our results clearly indicate that the differences in body size between the two species originate between metamorphosis and sexual maturity.

Keywords: food levels, growth efficiency, growth rate, metamorphosis, trade-off.

Introduction

Explaining and predicting variation in major life history traits, such as body size and growth of organisms is a major goal of life history theory (Kozlowski, 1992; Roff, 1992). In animals with indeterminate growth such as ectotherms, after reaching sexual maturity a trade-off in resource allocation occurs between reproduction and growth (Heino and Kaitala, 1999). Thus age and size at sexual maturity are key life-history traits since they affect growth rate and reproduction (Roff, 1992). They determine both how fast individuals within a population can start reproducing, but also how large their reproductive output (e.g., age-specific fecundity) will be. Since fecundity is often closely associated with body size (Plaistow et al., 2004), increased body size is usually accompanied by increased fecundity in females.

Growth rates are strongly dependent on food availability and quality (Blanckenhorn, 1999). Variation in growth rate and body size linked to food availability is widespread and generally predicted by life history models (Berri-gan and Charnov, 1994; Atkinson and Sibly, 1997). Growth rate influences individual fitness, and several studies have shown that high growth rates are linked to decreased starvation resistance (Dmitriew, 2011), competitive ability (Dahl et al., 2012), endurance to diseases (Vredenburg et al., 2010), but increased rate of skeletal ossification (Arendt, Wilson and Stark, 2001) and predation avoidance (Dmitriew, 2011; Orizaola et al., 2013).

Pond-breeding amphibians represent an ideal group for the study of life history traits trade-offs (Werner, 1986; Álvarez and Nicieza, 2002; Petranka, 2007). They have a complex life-cycle and show morphological adaptation combined with physiological and behavioral variability (Jørgensen, 1995). Variations in amphibian growth rate and body size are often stage and species-specific responses (Petranka, 2007). Most studies on amphibian size-specific growth are focused on larvae and adults, with few stud-

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ies targeting juveniles (Dare and Forbes, 2007). The study of postmetamorphic growth is important because it identifies the factors that control or influence size-specific growth at sexual maturity.

The European spadefoot toads (genus *Pelobates*) are highly specialized burrowing and strictly nocturnal species with a narrow ecological niche (Nöllert, 1990). Two related species occur in southeastern Europe (*P. syriacus* and *P. fuscus*), but their ranges overlap only in the Balkan Peninsula (Džukić et al., 2008; Iosif et al., 2014). A previous study of two syntopic populations from the Danube Delta Biosphere Reserve (Romania) showed that the two species differed significantly in body size and mass, and showed distinct sexual dimorphism. The females are significantly larger in *P. fuscus*, and males slightly larger in *P. syriacus* (Cogălniceanu et al., 2014). The study also revealed differences in age structure; *P. fuscus* was on average 5.0 years old, while *P. syriacus* was on average 7.4 years old. However, both species reached sexual maturity at a similar age. This suggested that differences in growth rates before sexual maturity and in energy allocation between growth and reproduction after sexual maturity, are likely due to variation in adult size in the syntopic species. Since larvae of spadefoot toad have a prolonged aquatic phase, upon metamorphosis they have a shorter period left before overwintering. Life-history theory states that rapid growth evolves when a minimum size must be reached quickly before overwintering (Arendt, 1997). Thus a high growth rate is expected in metamorphs during the few months left before winter, when anurans generally undergo their greatest growth (Labanick and Schlueter, 1976).

Metamorphs of the two spadefoot toad species are of similar size (Székely, 2010) and reach sexual maturity at a similar age, but at contrasting body sizes (Cogălniceanu et al., 2014). This indicates that there are species-

specific differences in growth rates. We hypothesized that the response to different feeding intensities and growth rates are species-specific. We conducted a laboratory experiment with three (high, medium and low) feeding intensity treatments to test how growth rate and efficiency of *P. syriacus* and *P. fuscus* metamorphs from syntopic populations are influenced by food availability.

Materials and methods

Experimental design

We collected 72 (36 *P. fuscus* and 36 *P. syriacus*) juveniles of similar size from Histria population (44°32'56''N and 28°45'56''E; Buică et al., 2013) in September 2013. We used wild-caught animals since captive bred metamorphs often start feeding late and after several months show an overall much wider range of body sizes than in the wild. We kept the juveniles in a laboratory in 4-liter plastic containers covered with soft plasticized mesh and filled with 6 cm of sand to provide adequate depth for burrowing. Each container had a small plastic cup constantly filled with water, and the sand was sprinkled daily. We provided natural photoperiod at constant temperature (20°C) and humidity (75%) conditions.

We used three feeding intensity treatments for each species: (i) high (feeding every other day), (ii) medium (feeding every three days) and (iii) low (feeding every six days). During the 98 days experiment the individuals in the intensive feeding treatment were fed 49 times, in the medium feeding treatment 25 times, and in the scarce feeding treatment 15 times.

In our experiment, we used 12 individuals of each species. Individuals were distributed among three replicate monospecific containers with four animals of the same species per container. Individuals were fed out of the container individually, to avoid interactions with others and keep a precise record of the amount of food consumed. Live insects were provided *ad libitum* for 10 minutes. Animals were individually identified based on their dorsal pattern, photographed at the beginning of the experiment (Gamble, Ravela and McGarigal, 2008).

We used as food five insect species from our captive-bred colonies: *Tenebrio molitor* larvae, *Blaptica dubia*, *Nauphoeta cinerea*, *Acheta domesticus* and *Gryllus assimilis*. The insects were provided alternatively, i.e. a single insect species was provided during a six-day period, identical in all treatments. In this way we provided a balanced diet, since the nutritional value of different insect species varies (Claussen and Layne, 1983).

The body mass of each individual was measured immediately before and after the feeding period, on an electronic balance (Triton T2 400), with a precision of 0.01 g. Every two weeks, we measured the snout-vent length (SVL), using a digital caliper with a precision of 0.01 mm. After the

end of the experiment the animals were kept in the laboratory until next spring when they were released at the site of capture.

Data analysis

Prior to analysis we tested for normality and homogeneity of variance by visual inspection of diagnostic plots of standardized residuals against normal scores and fitted values, respectively. To better meet normality and homoscedasticity assumptions, all response variables were natural log transformed.

Upon completion of metamorphosis, the juveniles grow isometrically or close (Jørgensen, 1989). Since body mass increased linearly in time both in *P. fuscus* ($R^2 = 0.95, 0.79$ and 0.69 for the high, medium and low intensity feeding treatments, respectively) and *P. syriacus* ($R^2 = 0.81, 0.77$ and 0.91), this allowed estimating growth rate as a linear relationship. We used two measures of growth rate. For each individual, we computed the difference between the final and initial body mass (g) divided by the 98 days of the study period. Similarly, we calculated the difference between the final and initial body length (mm) divided by the study period (Rist et al., 1997).

The amount of food consumed by each individual was calculated as the difference between body mass before and after feeding for each feeding event. We calculated an index of growth efficiency (i.e. the transformation of the food consumed in body mass) as the ratio between total amount of food consumed during the experiment divided by the increase in body mass (i.e. difference between final and initial body mass) (Rist et al., 1997).

We used linear mixed-effects models (LMMs) to test the effect of the feeding treatments and species on body mass, SVL, total food consumption, and growth efficiency. LMMs account for the correlated observations among the containers. In these models, the species and the feeding treatment were introduced as fixed factors and the containers were used as random factors. The models were fitted in R (R Core Team, 2013) using the nlme package (Bates, DebRoy and Sarkar, 2013). With the estimates from the model, pairwise comparisons between species and among treatments were made using the R multcomp package (Hothorn, Bretz and Westfall, 2008).

Results

The initial body mass and SVL did not differ significantly among juveniles in the three feeding treatments for both species (table 1). The initial body size differed significantly between the two species, with *P. syriacus* individuals larger in both body mass and SVL than *P. fuscus* (tables 1 and 2).

The species feeding treatment interactions were significant with respect to the total food

consumption, body mass increase, body mass growth rate and growth efficiency (table 1 and fig. 1). *P. syriacus* juveniles consumed more food, grew heavier and larger and increased faster in length and body mass and had higher growth efficiency than *P. fuscus*, except in the high food treatment for growth efficiency (fig. 1 and table 2). We found a significant main species effect on the final body mass and SVL and body length growth rate (table 1). Feeding treatment had a significant main effect on the final body mass but not on SVL (table 1).

The pairwise comparisons among feeding treatments indicated that juveniles of both species reared at high feeding intensity consumed more food than those from low (Tukey HSD test, *P. fuscus*: $z = -8.82, P < 0.001$; *P. syriacus*: $z = -6.46, P < 0.001$) and medium food treatment (*P. fuscus*: $z = -15.13, P < 0.001$; *P. syriacus*: $z = -11.36, P < 0.001$). The total food consumption was also significantly higher for juveniles reared at medium feeding intensity than those in low feeding treatment for both species (*P. fuscus*: $z = -6.30, P < 0.001$; *P. syriacus*: $z = -4.89, P < 0.001$). We found significantly higher final body mass in *P. syriacus* juveniles reared in high feeding conditions compared to juveniles in medium feeding condition ($z = -4.28, P = 0.001$). The body mass increase was significantly lower in low feeding conditions than in medium ($z = -2.95, P = 0.038$) and high ($z = -4.74, P < 0.001$) feeding conditions for *P. fuscus* and no significant difference in body mass increase among feeding intensity treatments was observed for *P. syriacus*. Juveniles of *P. syriacus* reared at high feeding intensity grew significantly faster in body mass than juveniles reared at low feeding treatments ($z = -4.75, P = 0.001$). Growth efficiency was significantly lower for *P. syriacus* juveniles in high feeding treatment than those in medium ($z = 3.60, P = 0.004$) and low feeding treatment ($z = 5.42, P = 0.001$) (table 1). Nevertheless, despite consuming higher amounts of food, growth rate did not vary. Instead, the index

Table 1. Effects of species and feeding treatments on total food consumption, initial and final body mass, body mass increase, initial and final SVL, body mass and body length growth rates and growth efficiency, analysed with linear mixed models and Type I ANOVA; : is the interaction effect.

	df	F	P
Initial body mass (g)			
Intercept	1, 64	371 311.600	<0.0001
Species	1, 64	21.500	<0.0001
Feeding treatment	2, 64	1.500	0.233
Species : Feeding treatment	2, 64	1.300	0.284
Initial SVL (mm)			
Intercept	1, 64	8546.664	<0.0001
Species	1, 64	70.049	<0.0001
Feeding treatment	2, 64	0.108	0.898
Species : Feeding treatment	2, 64	1.794	0.175
Total food consumption (g)			
Intercept	1, 64	3981.288	<0.0001
Species	1, 64	37.158	<0.0001
Feeding treatment	2, 64	176.861	<0.0001
Species : Feeding treatment	2, 64	3.632	0.032
Final body mass (g)			
Intercept	1, 64	14 759.237	<0.0001
Species	1, 64	94.906	<0.0001
Feeding treatment	2, 64	8.011	0.001
Species : Feeding treatment	2, 64	2.214	0.118
Body mass increase (g)			
Intercept	1, 64	157.313	<0.0001
Species	1, 64	24.706	<0.0001
Feeding treatment	2, 64	5.748	0.005
Species : Feeding treatment	2, 64	5.865	0.005
Final SVL (mm)			
Intercept	1, 64	35 420.000	<0.0001
Species	1, 64	70.500	<0.0001
Feeding treatment	2, 64	2.600	0.081
Species : Feeding treatment	2, 64	0.600	0.530
Body mass growth rate (g/day)			
Intercept	1, 64	4387.922	<0.0001
Species	1, 64	24.104	<0.0001
Feeding treatment	2, 64	5.747	0.005
Species : Feeding treatment	2, 64	5.834	0.005
Body length growth rate (mm/day)			
Intercept	1, 64	3438.688	<0.0001
Species	1, 64	19.029	<0.0001
Feeding treatment	2, 64	0.074	0.929
Species : Feeding treatment	2, 64	1.811	0.172
Growth efficiency (%)			
Intercept	1, 64	5161.785	<0.0001
Species	1, 64	8.447	0.005
Feeding treatment	2, 64	12.967	<0.0001
Species : Feeding treatment	2, 64	3.750	0.029

Table 2. Mean values over the three replicates of the experiment of the initial SVL and body mass, total food consumption, final body mass, body mass increase, final SVL, body mass and length growth rate, growth efficiency \pm SE (Standard Error) per species and treatment. In the brackets are the minimum and maximum values.

	<i>Pelobates syriacus</i>				<i>Pelobates fuscus</i>			
	High	Medium	Low	Mean	High	Medium	Low	Mean
Initial SVL (mm)	5.04 \pm 0.13 (4.27-5.69)	5.33 \pm 0.17 (4.42-6.06)	5.50 \pm 0.22 (4.31-6.82)	5.26 \pm 0.11 (4.27-6.82)	4.17 \pm 0.12 (3.61-4.95)	3.93 \pm 0.15 (3.18-5.01)	3.96 \pm 0.23 (2.61-5.06)	4.02 \pm 0.13 (2.61-5.06)
Initial body mass (mm)	34.76 \pm 0.48 (32.11-37.99)	35.67 \pm 0.48 (32.95-38.37)	36.13 \pm 0.57 (32.72-39.39)	35.52 \pm 0.3 (32.11-39.39)	33.76 \pm 0.27 (31.61-35.21)	33.17 \pm 0.54 (29.20-35.53)	34.04 \pm 0.53 (30.73-37.20)	33.65 \pm 0.27 (29.20-37.20)
Total food consumption (g)	9.203 \pm 2.118 (6.250-13.600)	5.939 \pm 2.247 (5.000-7.450)	4.337 \pm 1.072 (3.110-7.450)	6.490 \pm 2.671 (0.536-13.600)	8.257 \pm 1.330 (6.700-10.870)	4.621 \pm 0.536 (3.840-5.550)	3.083 \pm 0.532 (2.450-4.180)	5.320 \pm 2.361 (2.450-10.870)
Final body mass (g)	8.14 \pm 1.24 (5.91-9.80)	7.94 \pm 0.757 (6.50-9.29)	7.51 \pm 0.78 (6.02-8.87)	7.868 \pm 0.966 (5.91-9.80)	6.56 \pm 1.11 (5.25-8.60)	5.72 \pm 0.23 (5.30-6.24)	5.21 \pm 0.92 (4.05-7.00)	5.83 \pm 0.99 (4.05-8.60)
Body mass increase (g)	2.649 \pm 1.001 (0.970-4.360)	2.688 \pm 0.726 (1.810-4.360)	2.473 \pm 0.651 (1.750-4.360)	2.603 \pm 0.694 (0.970-4.360)	2.603 \pm 1.009 (1.130-3.880)	1.559 \pm 0.472 (0.820-2.420)	1.285 \pm 0.589 (0.230-2.380)	1.82 \pm 0.91 (0.23-3.88)
Final SVL (mm)	40.90 \pm 2.09 (37.03-43.75)	39.27 \pm 1.99 (36.03-43.54)	39.58 \pm 1.90 (36.21-42.31)	39.921 \pm 2.064 (36.03-43.75)	36.91 \pm 1.80 (34.17-40.35)	36.37 \pm 0.68 (35.17-37.43)	36.50 \pm 1.13 (34.91-39.09)	36.60 \pm 1.33 (34.17 \pm 40.35)
Body mass growth rate (g/day)	0.027 \pm 0.010 (0.010-0.044)	0.027 \pm 0.006 (0.018-0.037)	0.025 \pm 0.004 (0.017-0.034)	0.026 \pm 0.007 (0.010-0.044)	0.026 \pm 0.010 (0.011-0.040)	0.016 \pm 0.004 (0.008-0.024)	0.013 \pm 0.006 (0.002-0.024)	0.019 \pm 0.009 (0.002-0.040)
Body length growth rate (mm/day)	0.053 \pm 0.018 (0.024-0.097)	0.040 \pm 0.010 (0.028-0.057)	0.053 \pm 0.024 (0.000-0.092)	0.049 \pm 0.019 (0.000-0.097)	0.032 \pm 0.017 (0.008-0.060)	0.035 \pm 0.016 (0.012-0.066)	0.030 \pm 0.017 (0.011-0.060)	0.033 \pm 0.017 (0.008-0.066)
Growth efficiency (%)	28.280 \pm 7.290 (15.520-42.140)	45.400 \pm 8.750 (30.420-57.510)	58.200 \pm 12.480 (39.680-79.878)	43.964 \pm 15.632 (15.520-79.878)	31.030 \pm 10.210 (15.840-47.460)	33.870 \pm 9.510 (17.190-48.870)	40.660 \pm 14.540 (8.420-63.640)	35.19 \pm 12.02 (8.420-63.640)

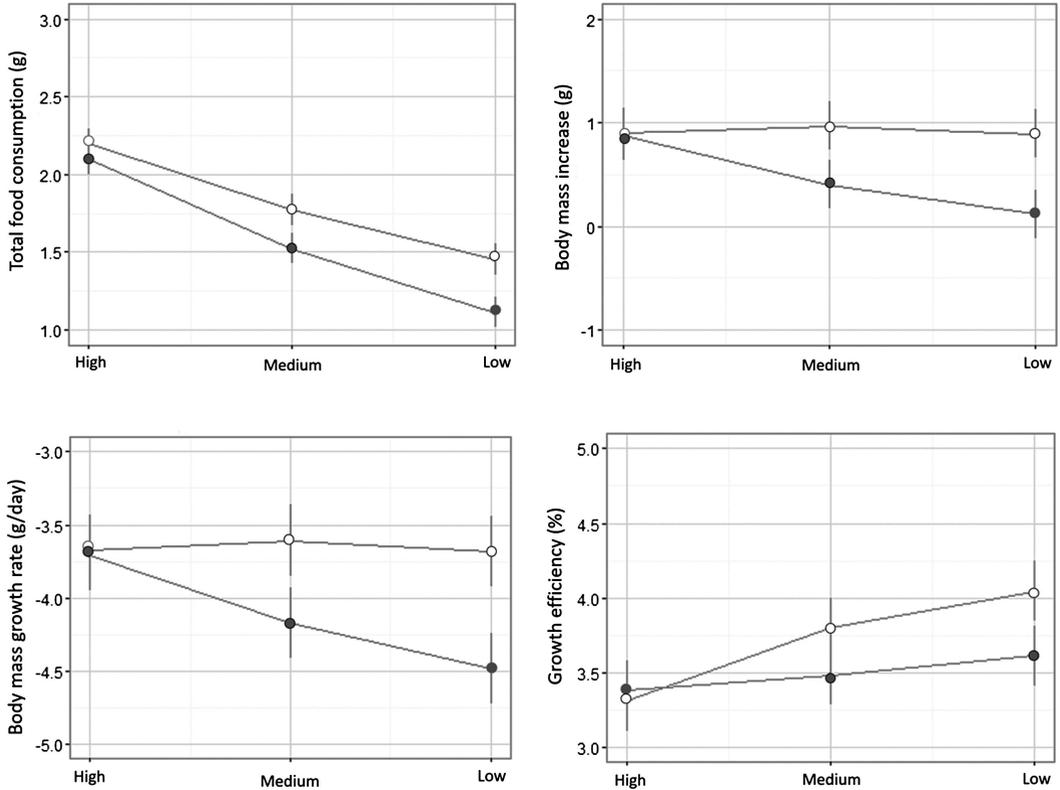


Figure 1. Interaction effect of species (*Pelobates syriacus* – open circles, and *P. fuscus* – closed circles) and feeding intensity treatment (high, medium and low), on predicted values of total food consumption (g), body mass increase (g), body mass growth rate (g/day) and growth efficiency (%).

of growth efficiency increased with decreasing food.

Discussion

Our study showed that the intensity of feeding affected both growth rate and growth efficiency, with juveniles in the high feeding treatment growing faster but with the lowest efficiency in converting consumed food in body mass. The two species differed in their response to food availability: *P. syriacus* juveniles have higher growth rate and growth efficiency values than *P. fuscus* juveniles. Also, *P. syriacus* juveniles responded to differences in feeding intensity by increasing growth efficiency with decreasing food levels. This adaptive strategy allows *P. syriacus* to maintain a relatively constant growth rate and reach similar body sizes,

independent of the food level. In contrast, *P. fuscus* had the same growth efficiency independent of the food availability and thus was directly affected by the decrease in food level. A similar study to ours on a North American toad (*Anaxyrus fowleri*) showed that the observed differences in juveniles' growth rate stemmed from the initial 21-day interval. Growth of the toads over the full nine-week period of the study increased linearly with prey biomass ingestion (Claussen and Layne, 1983). The authors found a temporal pattern in feeding, where the toads ate more after a three day fast than after two days fast. This suggests a complex behavioral and physiological pattern.

Individuals cannot benefit from both strategies (Arendt, 2009). Growth rates are influenced by environmental conditions like predation and

food availability. The former can have a significant impact on feeding since short-term foraging behavior is influenced by the risk of predation. Animals typically reduce the time spent foraging when predation risk increases (Ludwig and Rowe, 1990). Any changes in the time spent foraging involves trade-offs, in terms of energetic costs, exposure to predation and drought, but at the same time provides increased access to food.

Different juvenile growth rate, due to adaptive differences in either resource acquisition or allocation to basal metabolism, lead to different growth trajectories and sizes at a given age even before maturation (Enberg et al., 2012). Resource acquisition (including foraging, ingestion and digestion) controls the total amount of resources available to the organism, and these are allocated to various competing needs. A high growth rate will result in increased body size, and this will be advantageous only if the effect is decreasing adult mortality or increasing reproductive success (Brown and Sibly, 2006).

A comparative study of the two spadefoot toad species that examined their locomotor behavior showed that *P. syriacus* was significantly more active than *P. fuscus* (Székely et al., in press). This resulted in different patterns of foraging behavior, *P. fuscus* being more sedentary ('sit-and-wait') whereas *P. syriacus* is an active forager. This in turn suggests that *P. syriacus* achieves a larger size by having both higher growth efficiency and also increased food consumption due to a higher foraging effort. In the areas where the two species coexist, cases of cannibalism were recorded for *P. syriacus* (Székely et al., 2015), so predation by the larger *P. syriacus* on the smaller *P. fuscus* can be an important risk factor enhanced by the high density of the former. The long-term coexistence of related species with overlapping ranges is unlikely in the absence of ecological differentiation (Weissing, Edelaar and Doorn, 2011), but selection can reduce range overlap between species allowing long-term coexistence (M'Gonigle et al., 2012).

The two spadefoot toad species differ in adult body sizes and growth rates, with *P. syriacus* having larger adult body sizes and higher adult growth rate than *P. fuscus* (Cogălniceanu et al., 2014). Our study showed that these differences develop shortly after metamorphosis before reaching sexual maturity. Overall, our results show that *P. syriacus* is better adapted to variation in food availability than *P. fuscus*.

Acknowledgements. We thank D. Székely and F. Stănescu for help in collecting the juveniles, Dr. Onciu T.M. for useful advices during the experiment, Dr. B.R. Schmidt for useful suggestions on the data analysis, Dr. T. Hartel, Dr. M.J. Mazerolle and two anonymous reviewers for helpful comments on the early version of the manuscript. This work was supported by the Romanian National Authority for Scientific Research grant PN-II-IDPCE-2011-3-0173 to DC and the data analysis by PN-II-RU-TE-2014-4-1536 to RB. Animal collecting was possible thanks to the Danube Delta Biosphere Reserve Administration permit 3/21.02.2013. The experimental procedure was approved by the Ethics Committee of the Faculty of Natural and Agricultural Sciences, Ovidius University, Constanța.

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Submitted: January 21, 2016. Final revision received: November 12, 2016. Accepted: November 29, 2016.
Associate Editor: Marc Mazerolle.