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Preliminary overview of body condition variation among dice snake populations from transboundary Lake Prespa

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Abstract

Studies of body condition in snakes are generally lacking and were only done on a few species and with limited sample sizes. Additionally, almost no studies considered how different factors affect body condition. We used a large dataset amassed over a 15 year-long ecological study to make a preliminary screening of body condition index (BCI) variation in a metapopulation of dice snakes (*Natrix tessellata*) in the region of Lake Prespa. We considered how factors such as sex, food, colour morph, locality and time affect BCI. We demonstrate a positive effect of food (relatively less in males), and lower BCI in females. Importantly, there is a strong seasonal effect, summer months having a positive effect as opposed to spring. The results of our study raise important considerations for future studies on snake BCI, but also conservation of freshwater ecosystems.

Keywords: *Natrix tessellata*, colour morphs, conservation ecology, Golem Grad, Mal Grad, village Konjsko

Introduction

Many studies of animal ecology rely on estimating the body condition of different individuals in a population (Peig & Green 2009). When referring to body condition, we consider it to be a measure of the nutritional state of an individual animal, more precisely the amount of energy reserves such as fat and protein (Krebs & Singleton 1993; Schulte-Hostedde *et al.* 2001). Body condition is generally unfeasible to measure directly, because direct measurement requires destruction of the whole specimen (Weatherhead & Brown 1996; Reynolds & Kunz 2001). Therefore, many studies rely on non-destructive methods, usually based on body mass and linear measurements of body size to calculate a body condition index (BCI; Green 2001; Stevenson & Woods 2006). Several studies showed significant correlation between BCI and the absolute size of fat stores in animals (Ardia 2005; Schulte-Hostedde *et al.* 2005). As individuals with more fat stores are thought to be more likely to survive and reproduce (McGuire *et al.* 2018), BCI can potentially indicate the health of individual animals and is assumed to be related to fitness (Peig & Green 2009; McGuire *et al.* 2018). Keeping that in mind, BCI is of great practical importance to animal ecologists

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due to its strong associations with reproductive output (Guinet *et al*. 1998; Naulleau & Bonnet 1996) and survival (Burton *et al*. 2006; Reading 2007), among other traits.

Studies of BCI in snakes are generally lacking and were only done in a few species and with limited sample sizes (Bonnet & Naulleau 1994, 1995, 1996; Lind & Beaupre 2015). To our knowledge, only one study ever considered the effect of factors, such as sex and temporal effects on BCI in snakes (Coates *et al*. 2009). Nevertheless, these studies showed a strong relationship between fat body and liver reserves and BCI in all of the studied snake species. These results thus support the opinion that BCI can be used to estimate the amount of fat reserves and therefore the nutritional and/or health state of snakes (Weatherhead & Brown 1996; Falk *et al*. 2017). Body reserves in snakes influence several aspects of their biology such as reproduction (e.g., reproducing vs. only foraging for the season) and survival (e.g., intensity of foraging efforts) (Bonnet & Naulleau 1996; Lind & Beaupre 2015).

Additionally, snakes exhibit a great diversity of phenotypes both within and among species. This phenotypic variation could potentially be an important factor that affects BCI, as it was shown that distinct phenotype groups have certain evolutionary and ecological adaptations. Good examples of these adaptations are the trade-offs between melanistic and cryptic colour morphs of the European vipers in regard to the risk of predation, breeding propensity and post-partum mortality (Andrén & Nilson 1981; Capula & Luiselli 1994; Luiselli 1995). Therefore, studying the effect of different phenotypes on BCI, can potentially give us an important insight into ecological and evolutionary forces maintaining phenotypic diversity in a certain population.

Temporal effects should have a great impact on BCI in snakes as snakes have very distinct seasonal patterns of activity (Gibbons & Semlitsch 1987). In the case of dice snakes, each season is comprised of several phases which usually include vitellogenesis and spermatogenesis, spring mating, feeding, autumn mating and hibernation (Kärvemo *et al*. 2011), which could affect BCI differently and at different times. Changes in prey availability, population density, age and sex structure, along with factors such as anthropogenic threats and habitat degradation (Gibbons *et al*. 2000; Böhm *et al*. 2013) could potentially have a significant effect on BCI as well.
The aim of this study was to perform a screening of BCI in dice snakes in the transboundary region of Lake Prespa, while at the same time considering the effects of food, sex, colour morph, locality and temporal effects.

Material and methods

Study species

The dice snake, *Natrix tessellata*, is an amphibious, mainly piscivorous, and oviparous species of water snake (family Natricidae), widely distributed from western Europe and northern Africa, across Middle East and central Asia to eastern China (Gruschwitz *et al*. 1999). Where present, it is relatively common and often occurs in high population densities (Gruschwitz *et al*. 1999; Carlsson *et al*. 2011; Ajtić *et al*. 2013). Additionally, dice snakes exhibit a great diversity of phenotypes, both within and among populations (reviewed in Mebert 2011), which offers the opportunity to explore possible adaptations in distinct phenotypic groups.

Study site and sample

Lake Prespa is located on the Balkan Peninsula, in the transboundary zone between North Macedonia, Albania and Greece. The dice snakes here are highly abundant, likely due to abundance and diversity of fish species in Lake Prespa (Crivelli *et al*. 1997). In this region, dice snakes exhibit three distinct dorsal colour morphs (Figure 1A): dice (the most common pattern), concolour (represented with uniformly grey animals), and melanistic (Ajtić *et al*. 2013). Dice snakes were sampled at three localities in the Macedonian and Albanian parts of Prespa (Figure 1B): Golem Grad Island, Mal Grad Island and the coastal village of Konjsko.

Golem Grad

Golem Grad Island (GG; N 40°52'08'' E 20°59'23'') is located in the Macedonian part of Lake Prespa and is a strictly protected area within National Park "Galičica". The island covers an area of about 18 hectares with narrow rocky shores covered by bushy submediterranean vegetation and a plateau dominated by a forest of Greek juniper trees (*Juniperus excelsa*). Locally, it is often referred to as "Snake Island" due to the extremely dense dice snake population (~10 000 individuals; Ajtić *et al*. 2013). This seemingly prosperous population has been steadily declining in the past decade (pers. obs. from a 15-year-long capture-recapture study), likely due to great pressure from fish-poaching with fish-nets in which adult individuals entangle and drown in the dozens (Sterijovski *et al*. 2014).

Mal Grad

Mal Grad Island (MG; N 40°47'31" E 20°55'59") is situated in the Albanian part of Lake Prespa, in "Prespa" National Park. The island is very small (~5 ha) with an oval, barren plateau and several caves underneath. The shores are covered with small rocks with sporadic reed bed patches. Dice snakes seem to be abundant here, similar to Golem Grad; however further ecological studies are needed to discern population

Figure 1. A) All three morphs of dice snakes found in the Prespa region photographed on Golem Grad; from left to right: melanistic morph, dice morph and concolour morph; B) Sampling localities in the Lake Prespa region.

characteristics. Mal Grad was visited twice (2013 and 2021) and despite being a no-fishing zone, poaching was evident on both occasions (pers. obs.).

Konjsko village

Konjsko (KV; N 40°54′42″ E 20°59′26″) is an old fishing village, currently uninhabited apart from the summer tourist season. It is located on the western shore of Lake Prespa, in the Resen municipality of North Macedonia, and along with Golem Grad is a part of National Park "Galičica". The beaches are covered with small pebbles, ground up mollusc shells and sporadic patches of reed beds and willows (*Salix* sp.), and meadows and oak woodland (*Quercus* sp.) further inland. Here, the dice snake population faces high anthropogenic pressures such as intentional killing and poaching (pers. obs.). Studies on the dice snakes here were initiated in 2021.

Field protocol

In all three localities, snakes were captured by hand and kept in calico bags while awaiting measurement. We recorded the total and snout-to-vent lengths (to the nearest 0.1 cm), body mass (to the nearest 0.1 g), sex (based on the shape of the tail or hemipenis eversion when necessary), colour pattern, feeding status (by palpation or after regurgitation) and reproductive status in females (through palpation). Each individual on Golem Grad and in Konjsko was permanently marked using a modified technique of scale-clipping (Bonnet *et al*. 2002). Finally, snakes were released at their site of capture.

Sample

The complete sample used in this paper adds up to 5648 dice snakes: 43 individuals from Konjsko, 72 individuals from Mal Grad and 5533 (831 recaptures, 4702 individuals) from Golem Grad. Only the sample from 2021 contains snakes from all three localities (total of 185), the 2013 sample also contains 32 snakes from Mal Grad, while all the rest are from Golem Grad Island only. In light of these imbalances in sample sizes between the localities, the study is termed "preliminary" (particularly in respect to Mal Grad and Konjsko village). Inter-annually the sample is also imbalanced, mainly due to varying field effort.

Statistical analyses

BCI was calculated using residuals from a linear regression of ln-body mass (BM) against ln-snout-to-vent length (SVL) which has been demonstrated to be a reliable indicator of body reserves in snakes (Bonnet & Naulleau 1994, 1996). Using residuals minimizes the known bias of BCI in larger individuals (Peig & Green 2009). For the purpose of this study, we only used adult individuals i.e., females larger than 55 cm SVL, and males larger than 48 cm (Ajtić *et al*. 2013). In the adult cohort we modelled variation in BCI (numerical variable), initially, as a response to one of our categorical time variables: season (e.g. average BCI values for Summer 2008), year (e.g. average BCI values for 2008), month (e.g. average BCI values between all months of April 2008-2021), month within each year (MY, average BCI values separately for each April of the study period, e.g., April of 2008, April 2009, April 2010 etc.). We chose to first find the best "time" predictor as this variable can explain much variance as a proxy for (i) environmental variables, (ii) varying field effort and (iii) other obscure stochasticity. After finding the best time predictor (lowest AIC), we continued to model variation in BCI by adding the additive and/or interactive effects of sex (categorical variable), feeding status (categorical variable), and colour pattern (categorical variable). We excluded gravid females as the presence of eggs affects body mass and can thus affect BCI; gravidity was not modelled as an explanatory variable. We used generalized linear mixed models in order to model repeated measurements from recaptured individuals from Golem Grad as a random factor. We tested the effect of the random factor by comparing the model using all fixed effects and the random factor, with the same generalized least square model lacking the random factor (as suggested in Zur *et al*. 2009). We used a Stepwise Regression, with the Forward (i.e., Step-Up) model selection procedure (Sokal & Rohlf 1981). Competitive models were ranked through a model-selection procedure using Akaike information criteria (AIC) (Burnham & Anderson, 2002). Interactive effects with 'time' and some interactions with 'locality' could not be tested as the models failed to converge, likely due to significant imbalances in the sample (Table 1).

Finally, predictions were built from several models in order to best understand our data, viz-a-viz predictors of BCI, and in order to plot our results. Statistical analyses and graphs were produced in R using the packages 'stats' (R Core Team 2020), 'nlme' (Pinheiro *et al*. 2020) and 'ggplot' (Wickham 2016).

Results

Generalized linear mixed models

After model selection, the mixed model best-fit to our data explained variance in dice snake BCI using the interactive effects of locality with colour morph, and

Table 1. Breakdown of dice snake sample sizes per locality, sex and morph.

	Female			Male		
	Dots – Dice	Grey	Black	Dots - Dice	Grey	Black
Golem Grad	2755	1428	651	1457	709	458
Mal Grad	49	10	2	48	11	2
Konjsko village	33	10	4	25	10	2

sex with feeding status along with the additive effect of time ("month within each year", Table 2).

Exploration during model selection, demonstrated a significant temporal effect on BCI, between 'seasons' (Model rank 19, Summer>Spring [p=0.001]), 'years' (Model rank 20, with varying effects and significance factors), 'months' (Model rank 17, April>May [p=0.50]; April<June [p=0.00], July [p=0.00] & August [p=0.00], Figure 2D & 3C) and 'months within each year' (Model rank 16, with varying effects and significance factors). Since it drastically improves model fit (ΔAIC=789), in order to explore the effects of other explanatory variables we kept 'month within each year' as the best time predictor of BCI. This is particularly important since time and/or stochastic variation in BCI can confound other variables. For example, without time variation, females exhibit higher BCI on average, but our best-fit model infers an opposite trend [p=0.00].

As expected, animals with detectable food items in the stomach have significantly higher BCI than individuals without food (p=0.00). The grey and dots - dice morphs have a higher BCI than the black morph, but not significantly. The same insignificant trend is true for Mal Grad and Konjsko, compared to Golem Grad. Interestingly, our best fit model implied a significant interaction between feeding status and sex (p=0.00), such that in male snakes the positive effect of food is less pronounced than in females.

Discussion

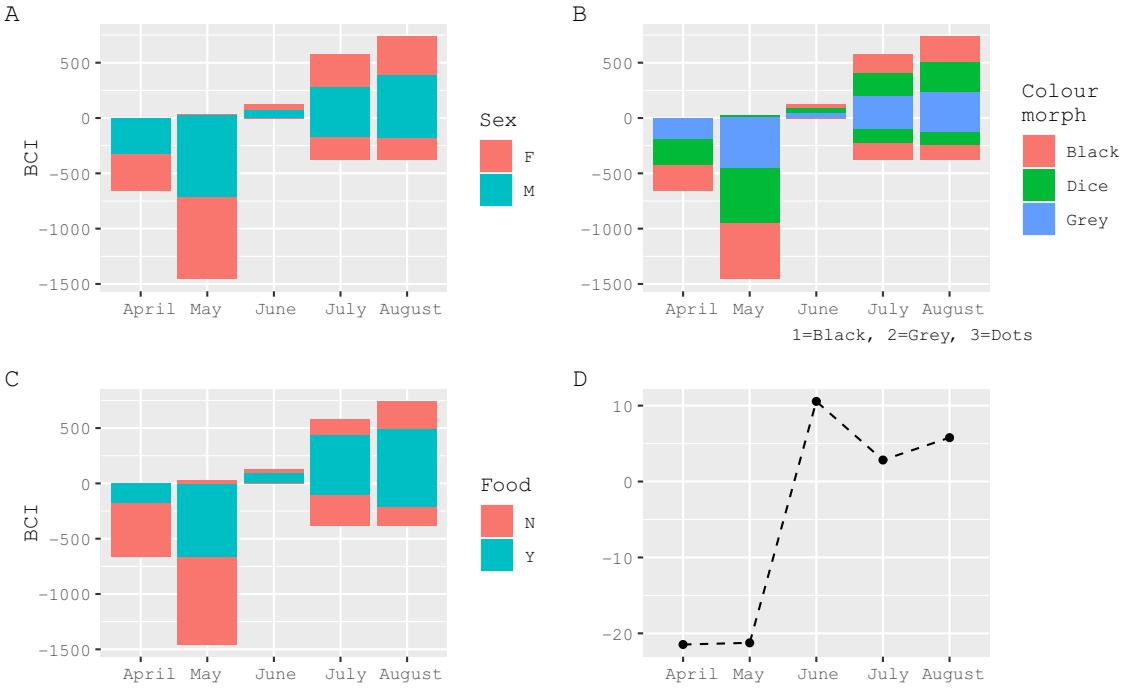
The results of this study showed how factors such as food, sex, colour morph and time impact variability in BCI at intra- and interpopulation levels. Our results support some hypotheses and results from earlier studies on snake BCI, but also offer insights into aspects that have not been considered previously.

Even though our data based on a large sample size show a significant time effect, it is difficult to interpret it in detail, due to the imbalanced sampling throughout the years and localities. The observed significant differences in BCI between all months of all years of sampling is probably not a result of inherent differences

Table 2. Model selection procedure of the competitive generalized linear mixed effects models built to explain variation in BCI of dice snakes from Prespa Lake, using additive (+) and interactive (*) effects of several potential explanatory variables. Model highlighted in black is the chosen best-fit model. AIC = Akaike information criterion; MY = Month within each year; CM = Colour morph; |IND = individual as random factor; model without 'IND' is a generalized least squares model.

Rank	Model	AIC
16	MY|IND	55970,4
17	Month|IND	56759,0
18	Season|IND	56814,0
19	Year|IND	57188,8
1	MY+Locality*CM+Food*Sex|IND	55751,0
5	MY+Locality*Food+CM*Sex|IND	55779,1
6	MY+Locality*Sex+CM*Food|IND	55782,9
2	MY+Locality+Food*Sex*CM|IND	55753,9
4	MY+Locality+Food*Sex+CM|IND	55772,2
7	MY+Locality+Food+Sex*CM|IND	55791,5
8	MY+Locality+Sex+Food*CM|IND	55791,7
21	Locality+Food*Sex*CM|IND	57515,9
9	MY+Food+Locality+Sex+CM|IND	55797,3
10	MY+Food+Locality+Sex|IND	55798,8
11	MY+Food+Locality|IND	55801,0
13	MY+Locality|IND	55918,0
14	MY+SEX|IND	55967,8
15	MY+CM |IND	55968,3
12	MY+Food|IND	55866,1
3	MY+Locality*CM+Food*Sex	55762,0

Figure 2. Variation in BCI as predicted (residuals) by the best-fit model (rank 1, Table 1) stacked in columns representing months; column colours demonstrate the samples of the interactive explanatory variables i.e., sex (A), colour morph (B) and feeding status (C); averaged (between months) predicted residuals from model rank 1 also presented to explicitely demonstrate monthly variation in BCI (D). F = females; M = males; Y = food is present N = food is not present; Colour morph: 1 = black, 2 = dice, 3 = grey



between the respective capture sessions i.e. "months within each year", but could rather be the effect of a plethora of different reasons such as: different field efforts, opportunities to visit different localities at only certain seasons or years, or capture probabilities, prey availability, population density, age and sex structure, weather effects and/or other stochastic effects at sampling instances. Nevertheless, when we stack this variation (month within each year) graphically (Figure 2A-C) and also present the predictions averaged by month (Fig. 2D) the seasonal effect on dice snake BCI is clear – snakes measured during the summer months (July & August) have a higher BCI (Figure 2D), regardless of sex, food presence or colour morph . In April and May (when BCI is at its lowest) snakes have just emerged from hibernation and will gradually begin to feed to restore the energy reserves spent over the winter. It was shown that dice snakes can lose up to 30% of body mass during hibernation (Velenský *et al.* 2011). Favourable hunting conditions usually occur in May (Carlsson *et al.* 2011; Velenský *et al.* 2011) and continue from that point onwards (throughout June, July and August) when a gradual rise in BCI values is evident. Finally, it seems to reach a plateau as the migration towards hibernation sites occurs and seasonal activities cease (Carlsson *et al.* 2011; Velenský *et al.* 2011).

Having conservation in mind, it is positive that all three countries of the basin impose a fishing ban (during the spawning season from the end of April until the beginning of June) when dice snakes come out of hibernation and start hunting intensely, but this is unfortunately not strictly enforced on the Albanian and Macedonian sides. Differences in management practices between countries justify further exploration of differences between localities. Our results imply Golem Grad dice snakes might be "worse off" than the other two sampling sites. Fortunately, the trend is not significant, thus the locality should continue to be closely monitored in order to untangle the true driver of this trend. Golem Grad enjoys the highest level of protection between the three localities; yet, this island lies almost exactly at the three-way border meeting point and it is closest to the Albanian mainland despite politically being part of North Macedonia. Consequently, control from its resident country is difficult to administer, while access for poachers from Albania is relatively easy (pers. obs.). Besides this supposed anthropogenic pressure, the effects of prey availability, different population density, variable microhabitats, predator pressure, etc. (Seigel *et al.* 1995; Gibbons *et al.* 2000; Böhm *et al.* 2013) could also impose variation in BCI. More data should be collected from Konjsko and Mal Grad in order to balance

the datasets and obtain insight that spans beyond only 2021.

Our data clearly shows a strong positive effect of food on BCI (Figure 2B). This result was expected as food presence in the digestive tract increases the animal's measured body mass, simultaneously artificially inflating the BCI of the individual (Weatherhead & Brown 1996). Further studies of BCI, especially those with conservational implications, should refrain from including animals with partially digested or undigested food items, or should rely on very large datasets that can overcome such potential biases.

The sexes, on the other hand, are balanced between localities; our results suggest that male dice snakes from Prespa have higher BCI than females (Figure 2A). When considering the reproductive and seasonal activity of each sex (Gruschwitz *et al*. 1999; Carlsson *et al*. 2011; Velenský *et al*. 2011; Ajtić *et al*. 2013), we assume that females should have lower BCI values than males. It was shown that gravid snakes are typically anorexic (Gregory *et al*. 1999); physiological suppression of appetite at a time when foraging might conflict with the more important function of thermoregulation for embryogenesis (Gregory 2014). After oviposition (usually in July (Carlsson *et al*. 2011; Velensky *et al*. 2011; Ajtić *et al*. 2013)), females tend to be severely emaciated (Bonnet & Naulleau 1994, 1995) and have limited time to forage before hibernation starts. The difference between males and females in BCI that we recorded could be driven by the aftermath of the reproductive season. Also, males are usually active earlier in the season and have more time to forage than females do (Carlsson *et al*. 2011; Velenský *et al*. 2011; Ajtić *et al*. 2013). When sufficient data allows for it, analyses should explore the interactive effect of 'sex' and 'season' on variation in BCI. Our results did point out a significant interaction between the presence of food and sex in dice snakes where the positive effect of food on BCI is less pronounced in males than in females. A simple explanation might stem from the well observed intersexual variation in diet composition between the sexes (Capula *et al*., 2011). Namely, larger snakes (females) can hunt larger fish, which in turn could have a more pronounced positive effect on BCI.

Melanistic individuals in our dataset seem to have lower BCI than the other two morphs, yet insignificantly. This alludes to possible fitness trade-offs of melanism, but the trend should be further explored once bigger datasets are collected also from Konjsko and Mal Grad. Melanism in snakes is thought to be beneficial, especially in the sense of efficient thermoregulation (Gibson & Falls 1979; Andrén & Nilson 1981). However, the melanistic phenotype is under higher predatory pressure (Andrén & Nilson 1981). Taking this into account, it is possible that melanistic snakes have limited foraging opportunities due to the supposed increased predator pressure and instead rely on their better thermoregulation and favour different foraging strategies (e.g. nocturnal activity (Mebert *et al*. 2011)).

Importantly, the results of our study can have significant conservation implications. We raise the notion that the dice snake might be considered as a reliable indicator of fish stock in Lake Prespa. As outlined by Durant *et al*., (2009) good indicator taxa should: (i) provide a representative picture of a certain process/effect monitored, (ii) respond rapidly to changes in the monitored process/effect while at the same time being easy to monitor, (iii) indicate the conditions on a large spatial scale. In other words, the response of the indicators in one or a few locations should indicate the state of the ecosystem in a larger area. It goes without saying that an indicator should have a reference value against which comparisons can be made. We feel strongly that dice snakes fill out most, if not all, of these traits/features. Next, the three examined populations are in close proximity to each other and can reflect changes in the entire transboundary area of Lake Prespa (Fig 1B). Moreover, dice snakes in all three localities are in high abundance and easily accessible; therefore easily monitored. Finally, our study provides a baseline for ongoing and future studies in this area.

In conclusion, we demonstrate an expected positive effect of food on BCI, while female dice snakes have lower BCI. Importantly, there seems to be a strong seasonal effect – summer months positively affecting BCI. This paper provides a suitable baseline for further and ongoing studies of snakes, particularly life-history studies. Moreover, using such variation as a reference baseline, we raise a very important notion of considering the dice snake as a potential reliable indicator of fish stock in Lake Prespa. Having in mind that Lake Prespa and its neighbouring Lake Ohrid have been identified as some of the most vulnerable ecosystems to climate change (Markovic *et al*. 2017), monitoring studies on dice snakes, and by extent, fish stock could prove important to the conservation of such freshwater ecosystems.

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