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Original paper

Duck body condition affects the number of parasites in the gastrointestinal tract, as evaluated with the Akaike information criterion

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ABSTRACT. The aim of the study was to determine the relationship between the body condition, and the number of parasites in the gastrointestinal tract of the tufted duck (*Aythya fuligula*), using the Akaike information criterion. Absolute and relative measurements of 197 ducks were taken. Liver mass was positively associated with the number of parasites in the duodenum (β = 0.5). Heart mass affected positively the number of parasites in the rectum (β = 2.3), the number of nematodes in the jejunum (β = 7.45), the total number of trematodes (β = 1.7), their number in the ceca (β = 7.3) and rectum (β = 4.2), and the number of cestodes in the ceca (β = 8.2). Beak length influenced the number of nematodes in the rectum (β = 1.7). Left tarsometatarsus length (β = 1.4) and relative head height (β = -2.0) affected the number of trematodes in the ceca. Tail length influenced negatively the number of cestodes in the ileum (β = -0.2). Similarly, a ratio of body mass to body length was negatively associated with the total number of parasites (β = -0.1), their number in the ceca (β = -0.2) and rectum (β = -0.3), the total number of trematodes (β = -0.3), and their number in the ceca (β = -0.5) and rectum (β = -0.4). A ratio of keel-skin length to keel length affected differently the total number of parasites in the ceca (β = 9.1), the number of nematodes in the jejunum (β = -17.9) and the number of trematodes in the duodenum (β = -5.8). A ratio of fat mass to body length affected the number of cestodes in the jejunum (β = 1.8). The present study indicates some morphological and anatomical parameters that may be useful for determining the correlation between the body condition and the level of parasitic infection.

Keywords: body condition, ducks, parasite-host interaction, Akaike information criterion, generalized linear model

Introduction

Body condition is a physiological state of an organism, strictly associated with its endurance and energetic efficiency [1]. It is described most frequently as either good or bad. In contrast to individuals in bad condition, animals in good condition have greater energy reserves [2]. Due to these reserves, their chance to survive and reproduce is higher. Besides estimating energy reserves, biochemical and physiological parameters are also used in studies on body condition by determining the level of hormones or blood metabolites [1]. Body condition state in free-living birds is very important since it affects the time of readiness for migration or temporary cessation of reproductive and moulting periods [3]. Research on the condition of free-living animals has mainly been carried out in such fields as ecology and environmental protection. The results of these studies contribute to the assessment of the state of the environment and populations of free-living animals in a given habitat. Therefore, it is possible to undertake actions aimed at population management through their monitoring, protection or limitation, as well as the management of their habitats [4].

Most studies on bird parasites and their influence on hosts describe their negative effect on body condition, body mass, energetic balance or reproductive period [4]. However, this relationship is not straightforward, since it is affected by external factors, including climate changes [5] and environmental pollution [6]. Despite a definitely negative effect of parasites on farm animal populations, their influence on those of free-living birds has not been fully characterized. In light of current research in ecology, the need for eliminating parasites from their natural ecosystems is not so obvious. Parasites are an integral part of natural environment and natural selection eliminates the most parasite-susceptible individuals from a host population. Together with the death of the host, its parasites, which too strongly affected a host organism and led to its death, die as well. Therefore, the most optimal situation for both sides of this relationship is a state in which there exists specific equilibrium between a parasite and a host and in which none of the partners significantly deteriorates the condition and decreases the number of the other [7]. It seems that the studies on the correlation between parasites and the body condition of free-living birds may contribute to the better understanding of the host-parasite relationship in the natural ecosystems.

One method of investigating the effect of body condition on the number of parasites is the use of the Akaike information criterion (*AIC*) [8]. It is increasingly popular in life sciences, especially in ecology [9]. An *AIC*-based approach allows for selecting an optimal model from the group of all the created models based on a relative distance (Δ_i) of these models from the best model [9]. This method differs from the classical approach based on the p-values, which indicate only the probability that the observed relationship can be attributed purely to chance.

Therefore, the aim of the present study was to determine the relationship between the duck body condition and the number of parasites in the gastrointestinal tract using the Akaike information criterion approach.

Materials and Methods

Parasites and hosts

Helminths (nematodes, trematodes and cestodes) were isolated from the digestive tract of 197 tufted ducks, (*Aythya fuligula*) (Anseriformes: Aythyini). All birds died in the fishing nets spread in Dąbie Lake. Due to the fact that the birds died on the same day (17.12.2013) and in the same place (53°28'09"N and 14°41'39"E), it can be assumed with high probability that they were the part of a larger population, which hatches, winters and feeds at the same site.

Among the investigated ducks, there were 69.0% (136) males and 31.0% (61) females. Adult birds (two years old and above) accounted for 86.8% (n = 171) of the total sample, whereas young birds for 13.2% (n = 26). Bird sex was determined during the section based on primary sexual characteristics (gonads), whereas age was assessed based on the body size and the patency of the bursa of Fabricius, which occurs only in young birds, i.e. in their first year of life.

Due to the analysis of dead animals, an ethical approval was not required.

Variables

Two sets of variables were used in the present study: the first one including the variables describing morphological traits (the measurements of individual body parts and their mass) and the second one including the variables describing the number of parasites from individual taxonomic groups, i.e. digenetic trematodes (Digenea), cestodes (Cestoda) and nematodes (Nematoda) found in the individual parts of the digestive tract. Within the first set of variables (some of which were suggested by the authors of the present study), the absolute measurements (such as length and mass) and relative ones (ratios of the length or mass of a body part or an organ to the total length or mass) were included. The relative measurements, i.e. indices, were used for describing the condition of the investigated ducks.

Among others, the following variables were used in the first set: relative tail length (RTL, %), relative left wing length (RWL, %), relative beak length (RBKL, %), relative head height (RHH, %), relative left tarsometatarsus length (RTTL, %), relative keel-skin length (RKSL, %), relative left pectoral muscle mass (RPM, %), relative liver mass (RLRM, %), relative heart mass (RHM, %), relative lung mass (RLM, %), relative kidney mass (RKM, %), relative visceral fat mass (RFM, %), body mass to body length ratio (BM/BL, g/cm), keel-skin length to keel length ratio (KSL/KL, mm/mm), kidney mass to body length ratio (KM/BL, g/cm), fat mass to body length ratio (FM/BL, g/cm).

In the second set, the variables describing the number of parasites from different taxonomic groups were included: Y_1 – the total number of parasites in the digestive tract, Y_2 – the total number of parasites in the proventriculus, Y_3 – the total number of parasites in the gizzard, Y_4 – the total number of parasites in the duodenum, Y_5 – the total number of parasites in the jejunum, Y_6 – the total number of parasites in the ileum, Y_7 – the total number of parasites in the cecum, Y_8 – the total number of parasites in the rectum, Y_9 – the total number of parasites in the cloaca and bursa of Fabricius, Y_{10} – the total number of nematodes in the digestive tract, Y_{11} – the number of nematodes in the proventriculus, Y_{12} – the number of nematodes in the gizzard, Y_{13} – the number of nematodes in the duodenum, Y_{14} – the number of nematodes in the jejunum, Y_{15} – the number of nematodes in the cecum, Y_{16} – the number of nematodes in the rectum, Y_{17} – the total number of trematodes in the digestive tract, Y_{18} – the number of trematodes in the duodenum, Y_{19} – the number of trematodes in the jejunum, Y_{20} – the number of trematodes in the ileum, Y_{21} – the number of trematodes in the cecum, Y_{22} – the number of trematodes in the rectum, Y_{23} – the number of trematodes in the cloaca and bursa of Fabricius, Y_{24} – the total number of cestodes in the digestive tract, Y_{25} – the number of cestodes in the duodenum, Y_{26} – the number of cestodes in the jejunum, Y_{27} – the number of cestodes in the ileum, Y_{28} – the number of cestodes in the cecum, Y_{29} – the number of cestodes in the rectum, Y_{30} – the number of cestodes in the cloaca and bursa of Fabricius.

The linear and mass measurements were taken according to Dzubin and Cooch [10]. The generalized linear models (GLM) with a negative binomial distribution of the dependent variable (the number of parasites) that described the relationship between the morphological and anatomical traits and the number of parasites were created. *AIC* allowed for the selection of the most adequate model out of the statistical models with a different number of explanatory variables. The best model was defined as one with the lowest *AIC* value [9,11]:

$$AIC = 2k - 2\ln(\hat{L})$$

where: k is the total number of parameters estimated in the model, $\hat{L}$ is the likelihood of the estimated model.

In practice, it is recommended to use the corrected value of *AIC* (AIC_C), since this criterion allows for the more accurate evaluation of the model quality and, with the sample size tending to infinity, AIC_C converges to *AIC* [11]. Therefore, this modified version of *AIC* was used in the present study [9]:

$$AIC_C = AIC + \frac{2k\ (k+1)}{n-k-1}$$

where k is the number of model parameters and n is the sample size.

When applying the *AIC*, it is not necessary to determine body condition groups (or classes, e.g. good, intermediate, poor). In this way, an intermediate stage of analysis (determination of body condition groups), which can significantly affect the final result, may be omitted. If the sample size is too small, there is a high probability that the *AIC* would allow for selecting the models with too many parameters. Hence, in order to avoid such a disadvantageous situation, it is recommended to use the so-called corrected *AIC* (*AICc*). Since in practice, *AICc* should be used in all cases (with the sample size tending to infinity, *AICc* converges to AIC), *AICc* was applied in the present study.

The first stage of an analysis based on *AIC* was the exclusion of all the explanatory variables that were highly correlated with other variables in order to avoid multicollinearity [9]. Next, in order to further reduce the set of explanatory variables, separate models were built, for each such a variable and their AIC_C values were compared with the null model (consisting only of an intercept). All explanatory variables whose AIC_C value was higher than that for the null model were excluded from further analysis, since it can be assumed in this case that such a variable did not significantly contribute to the explanation of the variability of the dependent variable (the number of parasites) [12]. Such a reduced set of explanatory variables was used for generating a series of models containing all the possible combinations of these variables [13].

Next, for each of the created models, the ΔAIC_C value was calculated (a difference between the AIC_C value of a given model and the model with the lowest AIC_C value in the analyzed set of models) [14]. In order to determine the probability with which a given model confirmed the hypothesis on an effect of the explanatory (body condition) variables on the explained variable (the number of parasites) [15], the weights (ωi) were calculated for all models whose ΔAIC_C value was lower than a threshold (equal to seven; models with a higher ΔAIC_C value were excluded from further analysis).

The weight value (the so-called model probability) indicated the probability with which a model corresponded to the best model (in terms of the Kullback-Leibler distance) [9]. In addition, the sum of weights ($\Sigma\omega i$) was calculated for each condition (explanatory) variable included in each of the created models describing a specific explained variable (the number of parasites), which allowed for determining a relative usefulness (importance) of a body condition variable for the description of the number of parasites [13].

For the evaluation of the strength and direction of an effect of the condition variable on the number of parasites, a model average of the beta coefficient (β) was calculated [16]. If this value was higher than zero, the relationship between the condition variable and the number of parasites was positive (when the value of the condition index increased, the number of parasites increased), whereas if the β value was below zero, the relationship was negative (when the value of the condition index increased, the number of parasites decreased). Finally, for each condition variable, an 85% confidence limit (CL) was calculated for the β coefficient in order to determine its real usefulness for describing the number of parasites. If the 85%-CL included zero, a given explanatory variable did not really affect the values of the explained variable, i.e. the number of parasites [12].

The following software was used in the present study for statistical analysis: Microsoft Office Excel 2010 (Microsoft Inc., Redmont, WA, USA), Statistica ver. 12 (StatSoft Inc., Tulsa, OK, USA), and R (R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

Results

The relationship between relative condition parameters and the number of parasites

After an initial analysis of hundreds of created models, six linear (relative) and six mass (relative) variables were selected (RTL, RHH, RBKL, RTTL, RKSL, RWL, RPM, RLRM, RHM, RLM, RKM and RFM). They were ultimately included in the models (Tab. 1). The models were created for the total number of parasites, individual taxonomic groups and gastrointestinal tract sections.

For the description of the total number of parasites, three models including RHM and RTL were selected (Tab. 1). Each of them corresponded to the best model describing the variability in the total number of parasites in the tufted duck with a similar probability (about 30.0%). An additional analysis of the sum of weights ($\Sigma\omega i$) showed that RHM and RTL determined the total number of parasites to a similar extent (63.0% and 56.0%, respectively; i.e. they had a similar relative importance) (Tab. 2). However, in contrast to RHM, RTL was negatively associated (β = -0.1) with the number of parasites (the total number of parasites decreased with an increasing RTL). Despite a relatively high importance of the analyzed variables, their 85% CLs for the β coefficients included zero, which means that they did not have any real effect on the total number of parasites in the tufted duck.

After creating a large number of models describing the relationship between the selected relative parameters and the total number of parasites in the consecutive sections of the gastrointestinal tract (Tab. 1), it was found that the analyzed traits had a real effect on the number of parasites only in two sections of the gastrointestinal tract, i.e. duodenum and rectum. For the description of the number of parasites in the duodenum, two models were ultimately selected ($\Delta AIC_C < 7.0$). The first model, which included RLRM corresponded to the best model explaining the variability in the number of parasites in the duodenum with a 70.0% probability ($\omega i = 0.7$). The value of the 85% CL (0.1–1.0) for the β coefficient indicated that RLRM positively ($\beta = 0.5$) affected the number of parasites in the duodenum (Tab. 2). The second model including RLM corresponded to the best model describing the variability in the number of parasites in this section with a 16.0% probability ($\omega i = 0.2$). However, RLM, in contrast to RLRM, did not have any real effect on the total number of parasites in the duodenum (85.0% CL from -0.6 to 0.9). For the description of the number of parasites in the second section (rectum) of the gastrointestinal tract, four models including three variables (RWL, RHM and RKM) were selected. Only one of them, including both RWL and RHM corresponded to the best model explaining this variability with a high probability ($\omega i = 0.7$). An additional analysis of the sum of weights, the values of the β coefficients and 85% CLs for RWL ($\Sigma\omega i = 0.8$; $\beta = -0.2$; 85.0% CL from -0.4 to 0.0) and RHM ($\Sigma\omega i = 0.8$; $\beta = 2.7$; 85.0% CL from 0.7 to 4.6) showed that both variables affected the number of parasites in the rectum to a similar extant, however, they differed in the direction of this relationship (negative for RWL and positive for RHM).

Table 1. *AICc* values for models describing the relationship between morphometric variables and indices and the number of parasites in the consecutive sections of the digestive tract

Digestive tract section	Model	*K*	*AICc*	*ΔAICc*	*ωi AICc*	*Dev*
Duodenum[1]	RLRM	3	958.24	0.00	0.70	952.12
	RLM	3	961.19	2.94	0.16	955.06
	Int	2	961.54	3.30	0.14	957.48
Duodenum[1]	BM/BL	3	959.99	0.00	0.69	953.86
	Int	2	961.54	1.56	0.31	957.48
Duodenum[3]	BM/BL, KSL/KL	4	819.22	0.00	0.47	811.01
	KSL/KL, KM/BL	4	821.27	2.05	0.17	813.06
	BM/BL	3	821.41	2.19	0.16	815.29
	KSL/KL	3	822.42	3.20	0.10	816.30
	KM/BL	3	823.04	3.82	0.07	816.92
	Int	2	824.37	5.15	0.04	820.30
Jejunum[2]	RLRM, RHM	4	92.52	0.00	0.60	84.31
	RHM	3	93.56	1.05	0.35	87.44
	RLRM	3	97.67	5.15	0.05	91.54
	Int	2	100.21	7.70	0.00	96.15
Jejunum[2]	KSL/KL	3	98.05	0.00	0.75	91.92
	Int	2	100.21	2.17	0.25	96.15
Jejunum[4]	FM/BL	3	1336.01	0.00	0.76	1329.89
	Int	2	1338.34	2.33	0.24	1334.28
Ileum[4]	RTL	3	1221.39	0.00	0.76	1215.26
	Int	2	1223.65	2.27	0.24	1219.59
Ceca[3]	RHH, RTTL, RHM	5	624.48	0.00	0.69	614.17
	RHH, RHM, RKM	5	627.89	3.40	0.13	617.57
	RHH, RHM	4	628.04	3.55	0.12	619.83
	RHH, RTTL	4	630.27	5.79	0.04	622.06
	RTTL, RHM	4	630.81	6.33	0.03	622.61
	Int	2	638.23	13.75	0.00	634.17
Ceca[4]	RHM, RKM	4	85.00	0.00	0.49	76.69
	RHM, RFM	4	85.43	0.43	0.39	77.22
	RBKL, RHM	4	98.78	4.77	0.04	81.57
	RPM, RFM	4	90.51	5.50	0.03	82.30
	RFM	3	90.97	5.97	0.02	84.85
	RHM	3	91.63	6.63	0.02	85.51
	Int	2	95.82	10.81	0.00	81.75
Ceca[1]	BM/BL, KSL/KL	4	1070.02	0.00	0.79	1061.81
	KSL/KL	3	1073.73	3.71	0.12	1067.61
	BM/BL	3	1074.42	4.41	0.09	1068.30
	Int	2	1080.08	10.06	0.00	1076.02
Ceca[3]	BM/BL, KSL/KL	4	629.98	0.00	0.48	621.77
	BM/BL	3	630.04	0.07	0.46	623.92
	KSL/KL	3	634.17	4.19	0.06	628.04
	Int	2	638.23	8.25	0.00	634.17

Table 1 con. *AICc* values for models describing the relationship between morphometric variables and indices and the number of parasites in the consecutive sections of the digestive tract

Rectum[1]	RWL, RHM	4	743.61	0.00	0.69	735.40
	RHM	3	747.35	3.75	0.11	741.23
	RWL	3	747.65	4.04	0.09	741.52
	RKM	3	748.54	4.93	0.06	742.41
	Int	2	748.80	5.20	0.05	744.74
Rectum[2]	RBKL, RLM	4	125.90	0.00	0.54	117.69
	RBKL	3	127.17	1.28	0.28	121.05
	RLM	3	128.75	2.86	0.13	122.63
	Int	2	130.74	4.84	0.05	126.68
Rectum[3]	RWL, RHM	4	648.19	0.00	0.75	639.98
	RHM, RKM	4	653.02	4.83	0.07	644.82
	RWL, RKM	4	653.34	5.15	0.06	645.13
	RHM	3	653.51	5.32	0.05	647.39
	RWL	3	654.12	5.93	0.04	648.00
	RKM	3	654.43	6.24	0.03	648.31
	Int	2	655.70	7.51	0.00	651.64
Rectum[1]	BM/BL	3	741.25	0.00	1.00	735.13
	Int	2	748.80	7.55	0.00	744.74
Rectum[3]	BM/BL	3	648.15	0.00	1.00	642.02
	Int	2	655.70	7.56	0.00	651.64
Total[1]	BM/BL	3	1956.59	0.00	0.78	1950.46
	Int	2	1959.14	2.55	0.22	1955.07
Total[3]	BM/BL	3	1480.66	0.00	1.00	1474.54
	Int	2	1494.47	13.81	0.00	1490.41

[1] – number of parasites, [2] – number of nematodes, [3] – number of trematodes, [4] – number of cestodes, Int – intercept, *K* – number of model parameters, *AICc* – value of the Akaike information criterion for small samples, Δ*AICc* – difference in the *AICc* values, *ωi AICc* – model weight, *Dev* – deviance

Also, the relationship between relative parameters and the total number of nematodes, trematodes and cestodes and their number in the consecutive sections of the gastrointestinal tract was analyzed (Tab. 1 and 2). The influence of these variables on the number of nematodes was only found in two sections of the digestive tract. i.e. the jejunum and rectum. For the description of the variability in the nematofauna of the jejunum, three models (Tab. 1) including RLRM and RHM were selected. The model with the highest probability of the proper explanation of the relationships between variables, included both RLRM and RHM (ωi = 0.6). Among them, RHM ($\Sigma\omega i$ = 1.0) determined the number of nematodes to a much greater extent than RLRM, being positively associated with this trait at the same time (β = 7.45; 85.0% CL from 3.8 to 11.1). In order to prepare three models describing the number of nematodes in the rectum, RBKL and RLM were used. The most probable model included two explanatory variables (ωi = 0.5), however, the value of the sum of weights and the CLs ($\Sigma\omega i$ = 0.6; 85.0% CL from -5.5 to 0.4) indicated a relatively small influence of RLM on the number of nematodes in the rectum. RBKL determined this trait to a much greater extent ($\Sigma\omega i$ = 0.8; 85.0% CL from 0.3 to 3.0), being positively associated with it at the same time (β = 1.7).

The relative biometric parameters considerably affected both the total number of trematodes and their number in the ceca and rectum (Tab. 1). RTL, RBKL, RTTL and RHM turned out to be relatively important traits in the nine models describing the relationship between the biometric variables and the total number of digenetic trematodes. However, none of the nine models explained the variability in the total number of these parasites with a high probability. Of the selected parameters, RHM and RBKL had the largest sum of weights ($\Sigma\omega i$ = 0.7) and were positively associated (β = 1.7; 85.0% CL from 0.2 to 3.1 and β = 0.5; 85.0% CL from 0.0 to 0.9, respectively) with the total number of trematodes (Tab. 2). However, the 85.0% CLs for RBKL and two remaining relative parameters included zero, which shows that they did not have any real influence on the variability of this trait. In order to describe the number of trematodes in the ceca, four relative parameters (RHH, RTTL, RHM and RKM) included in the five models were also used. Only one of them, including RHH ($\Sigma\omega i$ = 1.0; 85.0% CL from -3.1 to -1.0), RTTL ($\Sigma\omega i$ = 0.8; 85.0% CL from 0.3 to 2.5) and RHM ($\Sigma\omega i$ = 1.0; 85.0% CL from 3.8 to 10.9) explained this relationship with high probability (ωi = 0.7). A more detailed analysis of the model fit showed that all three relative parameters considerably affected the number of trematodes in the ceca, and that the association was positive for RTTL (β = 1.4) and RHM (β = 7.3) and negative for RHH (β = -2.0). Among the six created models describing the number of trematodes in the rectum, only one, including both RWL and RHM represented the best model describing this relationship with high probability (ωi = 0.8). Both variables ($\Sigma\omega i$ = 0.9) were relatively important in explaining the variability in the number of trematodes, however, only for RHM, the 85.0% CL did not include zero (85.0% CL from 1.8 to 6.6). The relationship between RHM and the number of trematodes in this microenvironment was positive (β = 4.2).

An analysis of the relationship between the selected condition parameters and the number of cestodes showed that they only affected the number of these flatworms residing in the ileum and ceca (Tab. 1 and 2). For the description of the first relationship, only one model (including RTL) with a relatively high probability (ωi = 0.8) of properly explaining this relationship was selected. A more detailed analysis of the model fit showed that RTL had a considerable negative association ($\Sigma\omega i$ = 0.8; β = -0.2; 85.0% CL from -0.4 to -0.02) with the number of cestodes in the ileum. For the description of the second relationship (between the condition parameters and the number of cestodes in the ceca), six models were selected. However, only two of them explained this relationship with a relatively high probability. The first model included RHM and RKM (ωi = 0.5), and the second one RHM and RFM (ωi = 0.4). Among three relative parameters included in these models, only RHM had a considerable positive influence ($\Sigma\omega i$ = 0.9; β = 8.2; 85.0% CL from 4.0 to 12.3) on the number of cestodes in the ceca.

The relationship between body condition indices and the number of parasites

After an initial analysis of hundreds of created models, four body condition indices were selected for further analysis: BM/BL, FM/BL, KSL/KL and KM/BL. As in the previous step, models were created for the total number of parasites, the number of parasites from each taxonomic group and individual sections of the digestive tract.

For the description of the total number of parasites in the digestive tract, only one model including one index (BM/BL) was selected. This model corresponded to the best model explaining the variability in the total number of parasites in the tufted duck with a 78.0% probability (ωi = 0.8), (Tab. 1) and the relationship between the variables was negative (β = -0.1) (Tab. 2). The CLs for this index indicated its real influence on the total number of parasites (85.0% CL from -0.2 to -0.02).

A more detailed analysis of the relationship between body condition indices and the total number of parasites in the consecutive sections of the digestive tract (Tab. 1 and 2) showed that such a relationship existed for the duodenum, ceca and rectum. In order to create a model describing the number of parasites in the duodenum and rectum, only one index (BM/BL) was used. In both cases, the value of the model probability (model weights) was high (69.0% and 100.0% for the duodenum and rectum, respectively). An additional analysis of the usefulness of the BM/BL index showed that it really affected only the number of parasites in the rectum (85.0% CL from -0.4 to -0.2), whereas in the duodenum, the 85.0% CL included zero (85.0% CL from -0.3 to 0.0), so its real influence on the number of parasites in the duodenum was null. These relationships in both cases were negative (β = -0.1, and β = -0.3 for the duodenum and rectum, respectively).

For the description of the number of parasites in the ceca, three models were selected including two aforementioned variables (BM/BL and KSL/KL), from which the highest probability was obtained for the model including both indices (ωi = 0.8). Based on the value of the sum of weights ($\Sigma\omega i$ = 0.9), it was found that both variables had a similar

Table 2. Relative importance of relative condition parameters and indices included in the models describing the number of parasites in the consecutive sections of the digestive tract (based on *AICc*)

Digestive tract section	Variable	∑*ωi AICc*	*β*	*SE*	-85% *CL*	+85% *CL*
Duodenum	RLRM[1]	0.70	0.52	0.32	0.06	0.97
	RLM[1]	0.16	0.19	0.51	-0.55	0.93
	BM/BL[1]	0.69	-0.14	0.10	-0.27	0.00
	BM/BL[3]	0.63	-0.14	0.10	-0.28	0.00
	KSL/KL[3]	0.74	-5.75	3.76	-11.16	-0.33
	KM/BL[3]	0.24	-2.20	4.25	-8.33	3.92
Jejunum	RLRM[2]	0.65	0.80	0.68	-0.17	1.78
	RHM[2]	0.95	7.45	2.52	3.83	11.08
	KSL/KL[2]	0.75	-17.88	11.87	-34.98	-0.79
Ileum	FM/BL[4]	0.76	1.80	1.12	0.19	3.40
	RTL[4]	0.76	-0.22	0.14	-0.43	-0.02
	RHH[3]	0.97	-2.01	0.73	-3.06	-0.96
Ceca	RTTL[3]	0.76	1.41	0.76	0.32	2.51
	RHM[3]	0.96	7.32	2.46	3.78	10.86
	RKM[3]	0.13	0.36	1.13	-1.26	1.99
	RHM[4]	0.94	8.19	2.88	4.05	12.34
	RKM[4]	0.49	-2.81	2.42	-6.29	0.67
	RFM[4]	0.45	-0.58	0.55	-1.37	0.21
	RBKL[4]	0.04	-0.08	0.39	-0.63	0.48
	RPM[4]	0.03	0.03	0.19	-0.24	0.30
	BM/BL[1]	0.88	-0.23	0.11	-0.38	-0.07
	KSL/KL[1]	0.91	9.06	4.40	2.72	15.39
	BM/BL[3]	0.94	-0.51	0.18	-0.77	-0.25
	KSL/KL[3]	0.54	5.72	6.69	-3.92	15.36
Rectum	RWL[1]	0.78	-0.22	0.13	-0.42	-0.03
	RHM[1]	0.80	2.67	1.37	0.70	4.64
	RKM[1]	0.06	0.10	0.46	-0.56	0.76
	RBKL[2]	0.82	1.68	0.93	0.34	3.01
	RLM[2]	0.67	-2.54	2.03	-5.46	0.38
	RWL[3]	0.85	-0.31	0.16	-0.54	-0.09
	RHM[3]	0.87	4.22	1.67	1.81	6.63
	RKM[3]	0.16	0.36	0.91	-0.95	1.67
	BM/BL[1]	1.00	-0.29	0.10	-0.44	-0.15
	BM/BL[3]	1.00	-0.35	0.12	-0.52	-0.18
Total	BM/BL[1]	0.78	-0.11	0.06	-0.20	-0.02
	BM/BL[3]	1.00	-0.30	0.07	-0.40	-0.19

[1] – number of parasites, [2] – number of nematodes, [3] – number of trematodes, [4] – number of cestodes, ∑*ωi AICc* – weight sums for models including the variable, *β* – estimated beta values, *SE* – absolute standard deviation, *CL* – confidence limit

contribution (similar relative importance) into the determination of the number of parasites in the ceca, and that KSL/KL affected this number positively (β = 9.1), whereas BM/BL negatively (β = -0.2). None of the CLs included zero (85.0% CL from -0.4 to -0.1 and from 2.7 to 15.4 for BM/BL and KSL/KL, respectively), which confirms the real influence of these indices on the number of parasites in this microenvironment.

In a similar way as for models including relative biometric parameters, the relationship between body condition indices and the number of parasites from individual taxa was verified, i.e. nematodes, trematodes and cestodes (Tab. 1 and 2), both as a total number and the number in the consecutive sections of the gastrointestinal tract. After an initial analysis of the $\Delta AICc$ values for the models describing the total number of nematodes (Tab. 1), none of them had this value below 7.0, which indicated the lack of influence of body condition indices on the total number of these parasites. Therefore, an analysis of the relationship between these indices and the number of parasites in the consecutive sections of the gastrointestinal tract was carried out. Three models were selected ($\Delta AICc$ = 0.0) for the description of the number of these helminths in the jejunum, cecum and rectum. A more detailed analysis of the role of these indices in the models (Tab. 2) showed their considerable influence only on the nematofauna of the jejunum (85.0% CL from -35.0 to -0.8). An index included in the model that represented the best model for the description of the variability in the nematofauna of this microenvironment with a 75.0% probability (ωi = 0.8) was KSL/KL, which was negatively associated with this variable (β = -17.9).

For the total number of trematodes in the digestive tract of the tufted duck, one model was selected (Tab. 1) which corresponded to the best model for the description of the analyzed relationship with a 100.0% probability (ωi = 1.0). It included only one index (BM/BL) which considerably and negatively affected the number of trematodes (85.0% CL from -0.4 to -0.2; β = -0.3) (Tab. 2). A more detailed analysis of the relationship between body condition indices and the number of trematodes in the consecutive sections of the gastrointestinal tract showed that these indices influenced the number of these flatworms in three microenvironments (duodenum, ceca and rectum). For the description of the number of trematodes in the duodenum, five models including three indices (BM/BL, KSL/KL and KM/BL) were initially selected. Each of them explained the variability in the number of trematodes in this section of the digestive tract with a probability not exceeding 50.0%. The weight of the best model including BM/BL and KSL/KL was 0.5. An analysis of the usefulness of individual indices showed that only KSL/KL had the real influence on the number of trematodes in the duodenum (85.0% CL from -11.2 to -0.3), and the relationship between the values of this index and the number of trematodes was negative (β = -5.8). This and another index (BM/BL) were included in the next two models, which represented the best model explaining the variability in the number of trematodes in the ceca with about 50.0% probability. A more detailed verification of the indices excluded KSL/KL (85.0% CL from -4.0 to 15.4), confirming the usefulness of BM/BL ($\Sigma\omega i$ = 0.9; 85.0% CL from -0.8 to -0.3) for the description of the variability in the number of trematodes in this section of the digestive tract at the same time. This last index, like in the previously analyzed section of the digestive tract, was negatively associated with the investigated trait (β = -0.5). BM/BL was also the only index included in the model describing the variability in the number of trematodes in the rectum and this relationship was negative (85.0% CL from -0.5 to -0.2; β = -0.4).

The last stage of the study involved an analysis of the relationship between body condition indices and the total number of cestodes in the whole digestive tract and its consecutive sections. Like in the case of the number of nematodes, none of the models reliably explained the variability in the total number of cestodes (Tab. 1). However, after a more detailed analysis, a relatively useful model for the jejunum (Tab. 1) was selected. It included one index (FM/BL), which positively affected (85.0% CL from 0.2 to 3.4, β = 1.8) the number of cestodes in this section of the digestive tract.

Discussion

After an initial analysis, six linear and six mass measurements as well as four body condition indices were included in the models. Among the afore-mentioned indices, only BM/BL affected the total number of parasites in the investigated tufted ducks. Moreover, this index also influenced the number of parasites in the duodenum, ceca and rectum. It is one of the most basic condition parameters besides body mass [3]. In contrast to the latter, it allows for comparing individuals of different size (e.g. males and females) [1], and better describes general body size and its proportions. A decreased ratio of body mass to body length is a good indicator of decreased energy reserves in the form of fat but it also indicates shortages of other components, such as proteins, which are essential for organism growth. Therefore, it can be assumed that this parameter describes bird body condition quite well. Decreased body condition may facilitate a higher level of parasitic infection [17]. Consequently, the fact that this index was negatively associated with the number of parasites should not be surprising. A similar relationship was also found for other parameters correlated with body size and energy reserves. An index proposed in the present study (KSL/KL), i.e. the parameter describing the thickness of integuments [18], and thus, subcutaneous tissue, which constitutes organism's energy reserves, was negatively associated with the number of nematodes in the jejunum and that of trematodes in the duodenum. In the literature, wing and tail lengths are also frequently used for describing body size or energy reserves [19,20]. They depend, to a large extent, on the process of moulting, which in turn requires large energy and protein reserves and so good body condition. Consequently, many authors use these parameters as an indicator of the general body condition of birds [3]. However, it should be mentioned that the usefulness of this parameter for body condition determination depends on bird species and it is not always well correlated with organism's energy reserves [20]. Nevertheless, it was found in the present study that RWL was negatively associated with the total number of parasites in the rectum and that RTL was negatively related to the number of cestodes in the ileum. The last parameter affecting the number of parasites was RHH, which was negatively associated with the number of trematodes in the cecum. Many authors have confirmed the association between head or skull size and body size of birds, thus RHH may play a role of a body condition indicator.

As already mentioned, better body condition may increase the chance of infection with some parasite species in some cases, due to more intensive foraging or more frequent migrations, among others [21]. So, it can explain the observed positive association between some body condition indices and the number of parasites. The FM/BL condition index, proposed in the present study, and the afore-mentioned KSL/KL index were positively associated with the number of cestodes in the jejunum and the total number of parasites in the ceca of the studied tufted ducks, respectively. Since they describe the level of fat cover in birds, they may serve as an indicator of energy reserves, and thus body condition of the investigated ducks. Based on such an assumption, it can be hypothesized that better body condition increased the number of cestodes in the jejunum and the total number of parasites in the ceca. A similar conclusion can also be made based on relative beak length (RBKL) and relative tarsometatarsus length (RTTL). These body parts are used for the description of body size or condition in many avian species [20]. According to [20], tarsometatarsus length, due to its low variability, may be the best morphometric predictor of body size and thus body condition.

Many authors state that the size of internal organs is correlated with bird size – indirectly indicating the general body condition of free-living animals [21]. The analysis showed a positive association between RLRM and the number of parasites in the duodenum and that between RHM and the number of cestodes in the cecum, the total number of trematodes, their number in the rectum, and cecum and the number of nematodes in the cecum. Many studies indicate a correlation between animal body size and heart mass [22] and liver mass [21] and thus indirectly the association between the mass of these organs and body condition of birds. It should, however, be mentioned that diseases such as cardiomyopathy, hepatitis, cirrhosis or neoplasms, undoubtedly decrease body condition, increasing organ mass at the same time [23]. Therefore, the interpretation of the positive correlation between the size of these organs and body condition of birds should be made with caution. In the present study, no visible signs of the afore-mentioned conditions in the investigated birds were found during the collection of organs (except for two cases of liver neoplasms, which were excluded from further analysis). Due to contradictory results on the correlation between the size of the above-mentioned organs and body condition, the correct and unequivocal interpretation of the obtained results may be impossible.

To sum up, a plethora of factors affecting parasitic infection makes the explanation of the relationship between body condition and the number of parasites quite difficult. Nevertheless, the present study indicates some morphological and anatomical parameters that may turn out to be useful for determining any association between the body condition and the intensity of infection with some groups of parasites. However, since not all the factors and relationships affecting parasitic infection are known, further research in this context is required.

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