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Exploring plastic-induced satiety in foraging green turtles☆

Robson G. Santos [a, *], Ryan Andrades [b], Guilherme Ramos Demetrio [c], Gabriela Miki Kuwai [a], Mañana Félix Sobral [a], Júlia de Souza Vieira [a], Gabriel E. Machovsky-Capuska [d]

[a] *Laboratório de Biologia Marinha e Conservação, Universidade Federal de Alagoas, Av. Lourival Melo Mota, s/n, Cidade Universitária, 57072-900, Maceió, AL, Brazil*

[b] *Laboratório de Ictiologia, Universidade Federal do Espírito Santo, Av. Fernando Ferrari, 514, Goiabeiras, 29075-910, Vitória, ES, Brazil*

[c] *Laboratório de Ecologia Vegetal, Universidade Federal de Alagoas/Campus Arapiraca – Unidade de Ensino Penedo, Avenida Beira Rio, s/n, Centro Histórico, 57200-000, Penedo, AL, Brazil*

[d] *The Charles Perkins Centre, The University of Sydney, NSW, 2006, Sydney, Australia*

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A B S T R A C T

In the last decade many studies have described the ingestion of plastic in marine animals. While most studies were dedicated to understanding the pre-ingestion processes involving decision-making foraging choices based on visual and olfactory cues of animals, our knowledge in the post-ingestion consequences remains limited. Here we proposed a theoretical complementary view of post-ingestion consequences, attempting to connect plastic ingestion with plastic-induced satiety. We analyzed data of plastic ingestion and dietary information of 223 immature green turtles (*Chelonia mydas*) from tropical Brazilian reefs in order to understand the impacts of plastic ingestion on foraging behavior. Generalized linear mixing models and permutational analysis of variance suggested that plastic accumulations in esophagus, stomach and intestine differed in their impact on green turtle's food intake. At the initial stages of plastic ingestion, where the plastic still in the stomach, an increase in food intake was observed. The accumulation of plastic in the gastrointestinal tract can reduce food intake likely leading to plastic-induced satiety. Our results also suggest that higher amounts of plastics in the gastrointestinal tract may led to underweight and emaciated turtles. We hope that adopting and refining our proposed framework will help to clarify the post-ingestion consequences of plastic ingestion in wildlife.

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1. Introduction

The menace of plastic pollution is recognized as a global problem having environmental, social and economic impacts. (Derraik, 2002; Newman et al., 2015). Today, plastic pollution has direct effects in over 600 marine species, many of these endangered, key to ecological processes and with value to local or global economy (Gall and Thompson, 2015). Although the number of species impacted by plastics is rising, ecological studies regarding the drivers involved in the ingestion of plastics and their fitness consequences remains limited (Browne et al., 2015).

In the last decade, several studies enlighten the influence of foraging strategies on plastic ingestion rates. Savoca et al., 2017, 2016) showed that the ingestion of plastics are likely influenced by infochemical cues that seabirds and fishes use to find their prey, and also the shape and color resemblance of plastic items with natural prey may partially explains the consumption in sea turtles and fish (Ory et al., 2017; Schuyler et al., 2012). Regardless to prey resemblance, debris coloration and brightness alters the conspicuousness of plastics to visual foragers (see Santos et al., 2016), which also influence the chance of ingestion. The likelihood of plastic ingestion in the ocean is also closely linked to the habitat use and opportunistic foraging behaviors of seabirds (Caldwell et al., 2019; Wilcox et al., 2015), sea turtles (Andrades et al., 2019; Santos et al., 2015a) and marine mammals (Alexiadou et al., 2019; Denuncio et al., 2011, 2017).

Previous studies in marine megafauna contributed to our understanding of plastic ingestion in relation to foraging behaviors. Thus, there is a major knowledge gap in our understanding of plastic ingestion susceptibility and potential post-ingestion effects

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* Corresponding author.
E-mail address: robson.santos@icbs.ufal.br (R.G. Santos).

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(but see Machovsky-Capuska et al., 2019; McCauley and Bjorndal, 1999a). Besides the physical consequences (e.g., intestinal blockage or perforation) derived from the ingestion of plastics, the reduce ability to acquire suitable food resources can lead to nutritional deficiencies in sea turtles (McCauley and Bjorndal, 1999a). Machovsky-Capuska et al. (2020), reported that estuarine green turtles (*Chelonia mydas*) with high ingestion of plastics had lower proportions of protein and water in their diets in comparison to reef turtles. The authors suggested that the nutritional niche of estuarine turtles was shaped by low availability of benthic food sources, high debris density and surface foraging strategies. In this context, gut fullness, body condition indexes and dietary information (including plastic ingestion) can be key variables helping to understand the mechanisms linked to satiety within plastic ingestion scenarios and their behavioral and fitness consequences (Lavers et al., 2014; Machovsky-Capuska et al., 2019).

Raubenheimer and Simpson (2019) noted that from a human perspective, "satiety" is the persisting sensation of repletion that results from eating. Although useful in the scientific study of animal nutrition, they suggested that careful consideration should be applied in the use of satiety considering that is an unobservable sensation that needs to be inferred from observable things. Thus, in a scenario of high food availability and nutritional diversity that enables an animal to reach their nutritional requirements, their gut fullness combined with dietary information can be a useful proxy for satiety. Herbivores like green turtles can select nutrient-rich food parts over those indigestible or nutritionally poor contents (Bjorndal, 1980; Illius and Gordon, 1993; Shantz et al., 2017), suggesting their likely ability to compose a diet balanced of specific nutrients that may promote satiety (Simpson and Raubenheimer, 2012). The carcasses of sea turtles and seabirds that contained plastics are often found in unhealthy conditions (i.e., emaciated or underweighted) (Lavers et al., 2014; Santos et al., 2015a). While there is a general agreement that the chronic ingestion of plastics may lead to negative fitness consequences and death (Baulch and Perry, 2014; Bjorndal et al., 1994; Fossi et al., 2018; Gall and Thompson, 2015; Lavers et al., 2014; Puig-Lozano et al., 2018; Schuyler et al., 2014), it remains to be established how plastic debris influences the feeding behavior and nutrient acquisition of marine animals (reviewed in Machovsky-Capuska et al., 2019). Increase feeding rates were experimentally reported by McCauley and Bjorndal (1999b), whereas Sturkie (1965) and Day et al. (1985) predicted satiety, appetite inhibition, reduce feeding intake, weight loss and nutrient deficiencies.

Here we combine stomach content analysis and body condition measurements to understand the impacts of ingested plastics on the foraging behavior of immature green turtles. In particular, we aim to: i) establish the relationship of food intake with plastic accumulation in esophagus, stomach and intestine; ii) explore whether the consumption of plastics influence the diet composition of green turtles; iii) evaluate the fitness consequences of plastic ingestion in relation to green turtles' body condition.

2. Methods

2.1. Sampling and data collection

We used diet and plastic ingestion data from 223 juvenile green turtles from reef areas in Brazil. The gastrointestinal tracts (GT) were obtained from stranded carcasses between 2009 and 2019 along the coast of Espírito Santo (ES) (20°16 'S, 40°17′ W), São Paulo (SP) (23°26′S, 45° 4′W) and Alagoas (AL) (09°39′S, 35°44′W), comprising a total of 8 geographic locations. Detailed information of the sampled animals relevant to this study can be found on the electronic supplementary material (ESM; Tables S1 and S2).

Necropsies and morphological measurements (i.e. curved carapace length -CCL-) were performed by veterinarians, following standard procedures (Wyneken, 2001). In order to establish the relationship of food intake with plastic accumulation in esophagus, stomach and intestine, we used a subset of our database ($n = 189$, for detailed information see ESM; Table S2), containing only individuals from 30 to 45 cm of CCL in order to reduce the effect of size on the total intake capacity. Considering that volume and weight of food items and plastics are highly correlated (Santos et al., 2015a, Santos et al., 2015b), we present our data using weight for increasing accuracy. As esophagus and stomach content items in green turtles presents low levels of digestion and are commonly used to evaluate diet (see Santos et al., 2015b), we used the wet weight of diet items found in the esophagus and stomach (measured using a digital scale of 0.01 g) combined as a proxy for total food intake. Plastics found in the GT were washed and dried at 60 °C for 48 h in order to increase weight accuracy. All plastics were subsequently quantified by weight (dry mass; digital scale of 0.01 g) and number of items (larger than 0.5 cm). Following Santos et al., 2015a, we established a minimum size of 0.5 cm for a debris item, as we consider that smaller pieces were generated from the fragmentation of larger items. Plastic fragments smaller than 0.5 cm were counted only in the total weight. Plastic pellets (raw plastic material from plastic products mostly around 1 mm) were considered as individual items, regardless of size.

To explore whether the ingestion of plastics influence the diet composition of green turtles, we used diet (relative biomass of main groups; Chlorophyta, Rhodophyta and Phaeophyceae) and plastic ingestion information from 60 animals.

Following Walsh (1999) the health of green turtles was classified as normal, underweight or emaciated using the plastron and eyes' characteristics, and the decrease in muscle and fat tissue in the neck and fore flipper area. As most of our turtles (97%) have ingested 5 g or less, individuals with plastic ingestion over 5 g were considered outliers following Quinn and Keough (2002). Therefore, we removed these individuals from our analysis, generating a subset of 136 green turtles.

2.2. Statistical analysis

The data obtained were separated in animals that ingested and that did not ingest plastic to observe possible differences. Due to the nature of the non-parametric data, the Mann Whitney test was used to make comparisons between these groups. In order to verify the influence of plastic ingestion on green turtle's food intake, we fitted generalized linear mixed models (GLMM), with a Gaussian error distribution and an identity link function for continuous data. These models were made using the 'lmer' function, from the package 'lme4' (Bates et al., 2015). We also used the 'dredge' function from the 'MuMIn' package (Barton, 2019) to test all possible combinations of the plastic ingestion variables included in the global model. To determine which of these variables were crucial in explaining changes in the sum of ingested food (weight of food found in esophagus and stomach), we used the lowest Akaike information criterion of second order (AICc) for small sample sizes (Burnham et al., 2011). A similar approach was applied to determine which variables were the vital in describing changes in the food quantity found in the esophagus, since food in this part of GT represents the last meal of an animal, therefore, it will be more closely related to foraging behavior prior death. Models with AICc$\leq$2 provide a related explanation power (Burnham et al., 2011), therefore, only them were presented in results. The Akaike information criterion of second order model weight (AICcWt) was considered the most parsimonious to answer our proposed research aims.

We tested for differences in diet composition variation, between animals which ingested plastic and those did not, using permutational analyses of variance (PERMANOVA) in ‘vegan’ package (Oksanen et al., 2019), considering each animal as an individual sample. The PERMANOVAs enabled to test for differences among algae items ingested by the turtles using environmental factors as predictors. In our case, we used the areas and the plastic ingestion as predictors. Tests were fitted considering all areas combined in order to verify the general effect of plastic ingestion, and also for each area to consider the differences of food availability among geographic areas.

To verify the influence of plastic ingestion on green turtle’s body condition we constructed a multinomial model using body categories (normal, underweight and emaciated) as response variables and the total amount of plastic in the GT as a predictor. In this sense, we used the normal body condition as a baseline to verify how plastic ingestion influenced body conditions. This test was based on the evaluation of the logs of the odds ratio, which represents the constant effect of a predictor on the likelihood that one outcome will occur (Quinn and Keough, 2002). In our analyses, a positive log of the odds ratio of the plastic ingestion would be related to the increase of the probability of a turtle to be in a worse body condition in relation to those classified as normal. In order to build the classification rule of our multinomial model, we first used a fraction of 30% of our dataset (i.e. training set), after that, we used this rule to test the classification of the remaining 70% of our dataset. All analyses were performed using the packages ‘dplyr’ (Wickham et al., 2019) and ‘nmet’ (Venables and Ripley, 2002).

All analyses were performed in the R software v 3.6.1 (R Core Team, 2019), for the analysis script see ESM.

3. Results

Food consumption relationship with plastic ingestion in different areas of the GT of green turtles was best described by our global model (Table 1). Food consumed was positively correlated with CCL and the amount of plastic found in the stomach and negatively correlated with the amount of plastic in the esophagus and intestine.

The CCL was consistently selected as the best model to explain the relationship the amount of food in the esophagus and plastic ingestion metrics (Table 2). However, the amount of food in the esophagus (highest AICcWt) negatively correlated with the amount of plastic in the intestine (lowest AICc).

Although diet composition varied with different geographic areas, no differences were observed on the diet between individuals that ingested plastic in relation to those that did not, between and within locations (Table 3). For detailed information on diet composition of green turtles in each area, please, see ESM, Table S3.

Turtles with normal body weight presented lower plastic amounts in the GT (0.07 g ± 0.19) when compared to underweight (0.24 g ± 0.88) and emaciated (0.82 g ± 1.46) turtles (ESM, Table S4). Our model presented a rate of 61% of correct classifications and showed that turtles with underweight (odds ratio = 3.49) and emaciated (odds ratio = 5.65) body conditions have higher plastic amounts in the GT, suggesting a negative relationship between these variables. In this sense, for each gram of plastic ingested, we may expect an increase in the probability (249%–464%) of a turtle to become underweight or emaciated when compared to those turtles that did not present any plastic in their GTs.

4. Discussion

A growing body of evidence describes the consumption of plastics in marine megafauna, yet few focused on their consequences (Colferai et al., 2017). Logistical challenges in collecting standardized data (e.g. mass) from regurgitations and stomach contents prevent researchers to move beyond isolated descriptions of the effects of debris in organisms (Gall and Thompson, 2015). Thus, as has been the case with other contaminants, it is important to consider the use of multiple measurements to provide predictive power and useful information for interpreting the effects of pollutants (Machovsky-Capuska and Raubenheimer, 2020; Underwood and Peterson, 1988). We combined proxies of behavior, physiology and fitness measurements to understand the consequences of ingesting plastic by immature green turtles.

While progress has been made on quantifying the mortality rates of species caused by plastics (Santos et al., 2015a; Schuyler et al., 2014), limited number of studies focused in sublethal effects and their associated impacts on the foraging behavior and health of organisms (Kühn et al., 2015; Lavers et al., 2014; Santos et al., 2015a). Food intake is regulated by a myriad of factors, from food availability and quality to predation risk (Hamilton, 2010; McCauley and Bjorndal, 1999b; Ydenberg, 2010). In areas where there is no strong influence of environmental stress and animals have access to suitable food items, the amount of food ingested is regulated accordingly with animals’ nutritional requirements (Machovsky-Capuska et al., 2016, 2020). Green turtles in most coastal areas may experience such scenarios, as sharks’ populations had sharply declining in last decades (Dulvy et al., 2014), there is a reduction in the predation risk pressure for this species, and tropical reefs usually have diverse food items (Santos et al., 2015b). Therefore, the intake of food is likely to be regulated by the quality of food available to green turtles in reef areas. Herbivore turtles actively consume plastics (Santos et al., 2015a) with no nutritional value that accumulate in the gut inducing a nutritional dilution (McCauley and Bjorndal, 1999a). It is, therefore, expected that a decrease of nutrients and energy available to the organism will lead to an initial increase in food intake (McCauley and Bjorndal, 1999b). We found that plastics in the stomach increased food intake, supporting previous suggestions.

Plastics found in the stomach have the potential to modified foraging decisions due to nutrient-specific deficiencies and plastic-

Table 1
Model selection between green turtle’s food intake and plastic ingestion metrics. Showing models with the AICc ≤2, plus the first model after this value. Intercept = Intercept value estimated for each model; CCL = Curvilinear Carapace Length (cm); P_{eso} = Amount of plastic found in the esophagus (g); P_{sto} = Amount of plastic found in the stomach (g); P_{int} = Amount of plastic found in the intestine (g); df = degrees of freedom; logLik = maximum likelihood; AICc = Akaike Information Criterion for small samples; ΔAICc = difference between the AICc of a given model and that of the best model; AICcWt = Akaike weights (based on AIC corrected for small sample sizes). Areas were used as random effect = (1 | loc), data = dados, na.action = “na.pass”). Variables values show coefficient estimates for each variable.

Global model = Sum of food amount in the esophagus and stomach ~ plastic amount in the esophagus (P_{eso}) + plastic amount in the stomach (P_{sto}) + plastic amount in the intestine (P_{int}) + Curvilinear Carapace Length + ((1 | loc), data = data, na.action = “na.pass”)									
Intercept	*CCL*	*(P_{eso})*	*(P_{sto})*	*(P_{int})*	*df*	*logLik*	*AICc*	*ΔAICc*	*AICcWt*
−432.2	14.47	−9.27	7.26	−3.17	7	−1117	2249	0	0.74
−427.6	14.3	−14.12	4.82		6	−1120	2252	3.31	0.14

Table 2
Model selection between green turtle's food amount in the esophagous and plastic accumulation in intestine metrics. Showing models with the AICc ≤2, plus the first model after this value. Intercept = Intercept value estimated for each model; CCL = Curvilinear Carapace Length (cm); P_{int} = Amount of plastic found in the intestine (g); df = degrees of freedom; logLik = maximum likelihood; AICc = Akaike Information Criterion for small samples; ΔAICc = difference between the AICc of a given model and that of the best model; AICcWt = Akaike weights (based on AIC corrected for small sample sizes). Variables values show coefficient estimates for each variable. Areas were used as random effect = ((1|loc), family = gaussian.

Global model = Food amount in the esophagus ~ plastic amount in the intestine (P_{int})+ Curvilinear Carapace Length + ((1|loc), family = gaussian)							
Intercept	*CCL*	*(P_{int})*	*df*	*logLik*	*AICc*	*ΔAICc*	*AICcWt*
−74.74	2.73	−0.87	5	−932	1874	0	0.56
−75.15	2.72		4	−933	1875	0.47	0.44
27.22		−0.84	4	−939	1887	12.64	0.01

Table 3
PERMANOVA results table for differences in diet composition variation between animals which ingested plastic and those did not. Tests were fitted considering all areas combined in order to verify the general effect of plastic ingestion, and also for each area to consider the differences of food availability among geographic areas. df: degrees of freedom; SS: sum of squares; MS: mean sum of squares; Pseudo-F: F value by permutation, P(perm): p-values based on 10,000 permutations. Significant differences marked in bold. Detailed information of the sampled animals and areas can be found on the electronic supplementary material (ESM; Tables S1 and S4).

Source	df	SS	MS	Pseudo-F	P(perm)
Considering all areas, and grouping animals by plastic ingestion in each area					
Group	5	3.99	0.80	5.44	< **0.01**
Residuals	55	8.06	0.15		
Total	60	12.05			
Considering all areas, without grouping animals by plastic ingestion					
Group	2	3.77	1.89	13.22	< **0.01**
Residuals	58	8.28	0.14		
Total	60	12.05			
Considering APACC-AL area, and grouping animals by plastic ingestion					
Group	1	0.07	0.07	0.45	0.71
Residuals	29	4.73	0.16		
Total	30	4.80			
Considering Aracruz/Fundão-ES area, and grouping animals by plastic ingestion					
Group	1	0.02	0.02	0.14	0.78
Residuals	17	2.16	0.13		
Total	18	2.18			
Considering Vitória-ES area, and grouping animals by plastic ingestion					
Group	1	0.12	0.12	0.96	0.36
Residuals	9	0.12	0.13		
Total	10	1.30			

induced satiation (Machovsky-Capuska et al., 2019). It is also possible that plastic-induced dilution could lead to a more generalist foraging behavior to achieve the nutritional and energetic requirements (Machovsky-Capuska et al., 2020). If nutritional dilution drives turtles to generalist feeding behaviors, these may increase the likelihood of plastic consumption (Andrades et al., 2019; Gusmão et al., 2016; Mizraji et al., 2017; Ryan, 1987). Although we were unable to detect diet differences in the presence/absence of plastics in the stomach of turtles, our analysis provided a potential foraging behavior pattern that should be further explored. Higher taxonomic resolution and nutritional data could be vital to elucidate this pattern.

High food intakes and fast transit regimes are expected for sea turtles inhabiting warm waters (Brand et al., 1999). The accumulation of plastic in stomach may limit the ideal food intake and may affect the success of foraging (Kühn et al., 2015). As plastic have a slower intestinal transit than natural prey (Clukey et al., 2017), it can be accumulated impairing digestive and physiological processes. The slower intestinal transit of plastic influences their accumulation in the GT, influencing foraging success and limiting the ideal nutritional intake of organisms (Kühn et al., 2015; Clukey et al., 2017). These combined effects are suggested to impede the digestion process leading to a feeling of fullness known as plastic-induced satiety (Kühn et al., 2015; Raubenheimer and Simpson, 2019). We found a negative relation between the plastic ingestion in the whole GT and food intake, in consistency with studies on seabirds (Azzarello and Van Vleet, 1987; Day et al., 1985; Kühn et al., 2015; Ryan, 1988) and invertebrates (Welden and Cowie, 2016).

Plastic-induced satiety that leads to a decrease in food intake may also cause deleterious impacts at cellular and systemic levels (Browne et al., 2015). This process often leads to nutritional deficiencies (Kühn et al., 2015; McCauley and Bjorndal, 1999b; Ponton et al., 2011), and an alteration in gut microbiome (Bjorndal, 1985; Bjorndal and Bolten, 1990), indicating underlying fitness consequences. In our study, we found that higher amounts of plastics in the GT negatively influence food intake that may lead to the observed emaciation and low body weight in turtles. Considering that animals are suggested to adjust food selection to strength their immune system (Ponton et al., 2011), we could assume that such unhealthy state may weaken their immune response increasing the risk of developing opportunistic viral infections (e.g. fibropapillomatosis) (Borysenko and Lewis, 1979; Santos et al., 2010). Given that plastic debris also carry additional pollutants (e.g. persistent organic pollutants and heavy metals) that are known for their negative physiological effects in individuals and populations (Teuten et al., 2009; Godoy et al., 2019), additional work is needed to explore the extent of their biological consequences in the health and immune systems of wildlife that have consumed them.

5. Conclusions

Overall, our study suggests that plastics consumed by immature green turtles accumulate in the GT generating a false sensation of fullness also known as plastic-induced satiety with negative

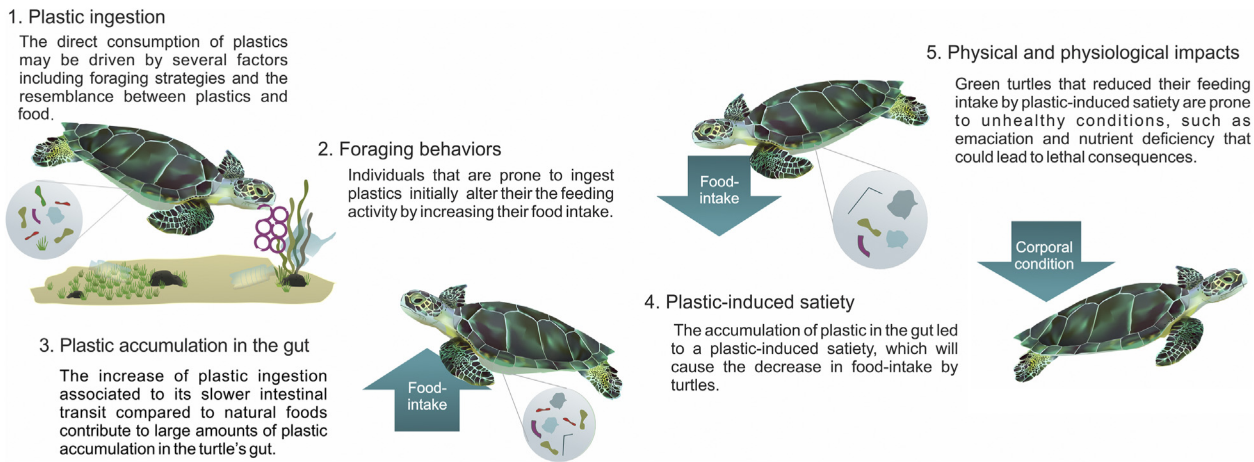

Fig. 1. Theoretical framework for post-ingestion acute and chronic effects of plastic ingestion by sea turtles.

ramifications to their food intake and foraging behavior, digestion process and body condition. We also provided evidence on the importance of a multi-level analysis to address the post-ingestion consequences of plastics in wildlife. To facilitate comparable studies, we proposed a framework (Fig. 1) that can be translate to marine, freshwater and terrestrial megafauna. Although these variables are hard to be tested in the field, controlled experiments and analyses of long-term datasets may contribute to test our predictions. Particular attention should be placed to behavioral, physiological and fitness characteristics of selected individuals and species (e.g. some animals may expel plastics in their feces, avoiding the accumulation of plastic in GT and their consequences). We, however, encourage future experiments to examine the potential progressive effects of plastic ingestion in feeding intake, nutrient-specific demanding, and body condition to gain a better understanding of the 'hidden' plastic ingestion impacts in wildlife.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Robson G. Santos: Conceptualization, Methodology, Investigation, Resources, Writing - original draft, Writing - review & editing, Supervision, Funding acquisition. **Ryan Andrades:** Conceptualization, Writing - original draft, Writing - review & editing. **Guilherme Ramos Demetrio:** Methodology, Formal analysis, Writing - review & editing. **Gabriela Miki Kuwai:** Data curation, Formal analysis, Writing - review & editing. **Mañana Félix Sobral:** Investigation, Data curation, Writing - review & editing. **Júlia de Souza Vieira:** Data curation, Visualization, Writing - review & editing. **Gabriel E. Machovsky-Capuska:** Conceptualization, Writing - original draft, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2020.114918.

Authors' contributions

R.G.S collected the data. G.R.D. and G.M.K. analyzed the data. R.G.S., R.A and G.M-C. wrote the manuscript with inputs from all authors. R.G.S designed the study. The authors do not have any conflict of interest to declare.

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