Recently-adopted foraging strategies constrain early chick development in a coastal breeding gull

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Human-mediated food sources offer possibilities for novel foraging strategies by opportunistic species. Yet, relative costs and benefits of alternative foraging strategies vary with the abundance, accessibility, predictability and energetic value of anthropogenic food sources, and to what extent such strategies ultimately result in fitness gain or loss, has important consequences for long-term population dynamics. Here, we studied the relationships between parental diet and early development in free-ranging, cross-fostered chicks and in captive-held, hand-raised chicks of Lesser Black-backed Gulls (*Larus fuscus*) breeding along the Belgian coast. This originally marine and intertidal foraging species is now increasingly taking advantages of human activities by foraging on terrestrial food sources in agricultural and urban environments. In accordance with such behavior, the proportion of terrestrial food in the diet of free-ranging chicks ranged between 4% and 67%, and consistent stable isotope signatures indicated that this variation was mainly due to between-parent variation in feeding strategies. A stronger terrestrial food signature in free-ranging chicks corresponded with slower chick development, however, no consistent differences in chick development were found when contrasting terrestrial and marine diets were provided *ad libitum* to hand-raised chicks. Results of this study hence suggest that anthropogenic diets may lower reproductive success due to limitations in food quantity, rather than quality.

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Abstract

Human-mediated food sources offer possibilities for novel foraging strategies by opportunistic species. Yet, relative costs and benefits of alternative foraging strategies vary with the abundance, accessibility, predictability and energetic value of anthropogenic food sources, and to what extent such strategies ultimately result in fitness gain or loss, has important consequences for long-term population dynamics. Here, we studied the relationships between parental diet and early development in free-ranging, cross-fostered chicks and in captive-held, hand-raised chicks of Lesser Black-backed Gulls (*Larus fuscus*) breeding along the Belgian coast. This originally marine and intertidal foraging species is now increasingly taking advantages of human activities by foraging on terrestrial food sources in agricultural and urban environments. In accordance with such behavior, the proportion of terrestrial food in the diet of free-ranging chicks ranged between 4% and 67%, and consistent stable isotope signatures indicated that this variation was mainly due to between-parent variation in feeding strategies. A stronger terrestrial food signature in free-ranging chicks corresponded with slower chick development, however, no consistent differences in chick development were found when contrasting terrestrial and marine diets were provided *ad libitum* to hand-raised chicks. Results of this study hence suggest that anthropogenic diets may lower reproductive success due to limitations in food quantity, rather than quality.

Introduction

Human activities globally provide a growing amount of food subsidies to free-ranging populations of animals, such as through household waste in cities, open-air landfills, or marine fishing discards (Oro et al. 2013; Real et al. 2017). Opportunistic feeders, i.e. species that vary their diet with local food availability, are at the centre of ecosystem responses to such subsidies as they can potentially switch to novel resources (e.g. Tornberg et al. 1999; Sorace and Gustin 2009). Still, the diversity of anthropogenic food subsidies implies that opportunistic species must choose amongst a range of potential foraging strategies, and thereby either adopt a generalist feeding strategy (true generalists sensu Andrén et al. 1997), or specialize on a distinct food source (Bolnick et al. 2003; Araújo et al. 2011; Dall et al. 2012). While specialization reduces intraspecific competition (Bolnick 2001), individuals relying on any particular anthropogenic food source are also exposed to fluctuations in food availability through changes in human activities (e.g. Pons 1992; Steigerwald et al. 2015). The adaptive value of alternative foraging strategies thus depends on the abundance, accessibility (i.e. energetic costs associated with foraging), predictability, and energetic value of anthropogenic food sources.

Many large gull species of the genus *Larus* make growing use of human-dominated (i.e. urban and agricultural) habitats for both feeding and breeding, albeit to a variable degree between and within breeding colonies (e.g. Garthe et al. 2016; Huig et al. 2016; Moreno et al. 2010; Shaffer et al. 2017),. Within single colonies, some breeders specialize on either marine or terrestrial food sources, whereas others consistently adopt more generalist strategies (Camphuysen et al. 2015;

Van Donk et al. 2017). While intra-population niche partitioning in gulls has been earlier linked to sex, age and personality (Navarro et al. 2010, 2017), reported effects on chick development of terrestrial vs. marine diets, or of specialist vs. generalist feeding strategies, are highly heterogeneous among studies (see e.g. Annett and Pierotti 1999; Hunt 1972; Pierotti and Annett 1991; Van Donk et al. 2017; Weiser and Powell 2010). It therefore remains unclear whether, and to what extent, newly-adopted terrestrial foraging strategies may either impose fitness costs or fitness benefits, to coastal breeding gulls.

Over the last decade, many populations of Lesser Black-backed Gulls (*Larus fuscus*) have shifted their foraging niche towards more terrestrial diets (Bicknell et al. 2013). Such consistent, large-scale niche shifts may either be driven by an overall decrease in marine food resources due to a decline in the local availability of fishery discards (Votier et al. 2004; Zeller and Pauly 2005), or reflect a niche expansion following local cultural evolution (sensu Danchin et al. 2004) due to the availability of new breeding and feeding opportunities inland (e.g. Noss et al. 2016; Newsome et al. 2015). Both hypothetical drivers imply different expected costs associated with terrestrial foraging. If terrestrial niche shifts are mainly driven by the need for alternative food sources by otherwise marine foragers, they are likely to imply fitness costs (O'Hanlon et al. 2017). However, the latter is not necessarily the case under niche expansion to previously unused food resources.

To disentangle potential effects of parental diet composition on chick growth from other environmental factors affecting individuals in natural populations, such as variation in food availability, we here report on a two-year field study on cross-fostered and synchronized free-ranging chicks integrated with an experimental dietary study on hand-raised chicks in nearby outdoor aviary facilities. Diets of free-ranging chicks were determined by means of carbon and nitrogen stable isotope analysis of feather samples, while hand-raised chicks were provided with either a pure terrestrial or marine diet *ad libitum*. Body condition and growth was based on repeated measures until 30 days of age for both groups of chicks. Earlier studies showed that growth rates and body mass during chick development are positively correlated with future survival rates (Lindström 1999; Stienen et al. 2002; Braasch et al. 2009; Bosman et al. 2016), and hence can act as proxy for fitness costs of parental foraging strategies.

Materials & Methods

Field study

We studied the development of free-ranging chicks in a mixed breeding colony of Lesser Black-backed Gulls and Herring Gulls (Larus argentatus) at the outer port of Zeebrugge (Belgium, 51°20'53"N 3°10'20"E). The colony counted 1458 L. fuscus pairs in 2016 and 1326 pairs in 2017 (Stienen et al. 2017, 2018.). Lesser Black-backed Gulls exhibits a limited sexual dimorphism (males being on average larger than females but with a large overlap) and shows bi-parental care. The species lays 2-3 eggs during May and June, of which the first two are largest (Verboven et al. 2005). At the onset of breeding in 2016 and 2017, 17 and 6 nests were randomly selected for monitoring and enclosed with chicken wire, respectively. Sample size was reduced in 2017 to avoid further disturbance of the colony after a year with high nest predator pressure. Each selected nest was visited every first, third and fifth weekday.

At the estimate day of hatching, experimental nests received first- or second-laid eggs of equal developmental stage (= pipping eggs), each originating from a separate nest to ensure hatching synchrony, thus preventing survival differences due to hatching asynchrony within and among clutches and ruling out effects of parental genetic quality on chick development. On the hatching day, nestlings were individually marked with coloured tape, and down feathers were collected for molecular sexing. During each visit, chick body mass (to the nearest g) and head length (to the nearest mm) were measured. At 30 days of age, the right innermost primary feather (P1) of each monitored chick was plucked and stored for isotope analysis.

Aviary experiment

To avoid unnecessary disturbance of the Zeebrugge colony, eggs for the aviary experiment were collected from a nearby gull colony in the port of Ostend (Belgium, 51°13'15"N 2°56'27"E) on 29 May 2016. We consistently collected one of the two largest eggs (i.e. first or second laid egg) from randomly selected 3-egg clutches. Chicks hatching from larger eggs have a higher chance of successfully fledging at 30-40 days after hatching (del Hoyo et al. 2018). To avoid laying date effects and ensure synchronized hatching, pipping eggs were sampled only. All collected eggs were placed in an incubator (temperature 37.5ºC, humidity 62%) in a nearby aviary facility of Ghent University hosted in the Ostend Bird Rescue Center (VOC Oostende) until they were fully hatched. A total of 20 chicks hatched between 30 May and 4 June 2016. At hatching, chicks were randomly assigned to a diet of either grinded full adult chicken (Gallus gallus domesticus) or grinded full Sprat (Sprattus sprattus), with 10 chicks per diet treatment. These food types were chosen based on their macronutrient composition, representative of the food items found in regurgitates of chicks at the colony of Zeebrugge (see Appendix). Loss of vitamins C and B1 due to prolonged deep-freeze storage was compensated by adding these to the thawed food. Food items were thawed at room temperature 6 to 8 hours before feeding the chicks. During the whole duration of the experiment, food was available *ad libitum* and refreshed every 3 hours between 9 AM and 9 PM. Chicks were measured every 5 days starting on the day of hatching, and until 40 days of age. Measurements comprised body mass (measured to the nearest g), total head length (head and bill, measured to the nearest 0.1 mm) and length of the external part of the P1 feather (measured to the nearest mm with a digital caliper). At 40 days of age, the P1 feather was plucked and stored for stable isotope analysis.

Sexing

All field and aviary chicks were molecularly sexed using DNA samples extracted from down feathers. A polymerase chain reaction (PCR) was performed using Fridolfsson and Ellegren (1999) 2550F/2718R primers, and sex was subsequently determined by electrophoresis of these samples.

Diet assessment

We estimated the terrestrial versus marine component in the diet of field chicks by means of carbon and nitrogen stable isotope analysis of feather samples, a technique that has proven efficient in assigning the proportion of assimilated diet components to a restricted number of sources in gulls, marine food being characterized by higher values of δ13C and δ15N than terrestrial food (Moreno et al. 2010; Steenweg et al. 2011; Weiser and Powell 2011). First, we assessed the local diet of Lesser Black-backed Gulls based on an analysis of 48 pellets and regurgitations of individuals breeding at Zeebrugge (Research Institute for Nature and Forest, unpubl. data 2006-2013), supplemented by literature data (Camphuysen 2011; Garthe et al. 2016). Based on this information, we collected and analyzed three samples of locally sourced swimming crabs (Subfam. *Polybiinae*), chicken meat, fish (Cod *Gadus morhua*, Sole *Solea solea*, Plaice *Pleuronectes platessa*), earthworms and fried potatoes. All food samples were freeze dried, ground and subjected to Accelerated solvent (ASE) lipid extraction as described in Bodin et al. (2009). Second, we cut P1 feathers of free-ranging chicks into 3 sections, each corresponding to a 10-day period. The length of feather sections in field chicks was estimated as the average length of P1 feathers in aviary chicks at 10, 20 and 30 days after hatching. Only feather vellum was used in the analysis of stable isotope ratios. All feather sections were cleaned 5 minutes in an ultrasonic bath, left 12 hours in a 2:1 chloroform –methanol wash, and oven-dried at 50 °C for 24 hours. After this, food and feather samples were finely cut and placed in tin cups. Third, isotopic ratios were obtained by mass spectrometry at the Department of Applied Analytical and Physical Chemistry of Ghent University. Isotope ratios are reported in per mil (‰) using standard delta notation:

$$\delta = \left[\left(\frac{Rsample}{Rstandard}\right) - 1\right] x\ 1000$$

where R represents the 13C/12C or 15N/14N ratio. Standards were Vienna Pee Dee Belemnite for carbon or air N2 for nitrogen, respectively. Fourth, stable isotope signatures in feathers were corrected for tissue fractionation by means of Trophic enrichment factors (TEFs). TEFs were calculated for carbon and nitrogen (δ13C and δ15N) between fish and chicken fed to aviary chicks, and the P1 feathers of these chicks, following Hobson and Clark (1992): δX = δa - δd, where δX = TEF for a given stable isotope, δa = stable isotope composition of feather vellum tissue and δd = stable isotope composition of the diet (see Appendix Table 5). The proportion of terrestrial food in the total chicks’ diet was estimated by Stable Isotope Analysis (SIAR, Parnell and Jackson 2013) in R (R Core Team 2018).

Data analysis

The estimated proportion of terrestrial food in the diet of field chicks was compared between age periods (0-10, 10-20, and 20-30 days after hatching) and sexes, by means of a beta regression with identity link (Ferrari and Cribari-Neto 2004) using R package betareg (Cribari-Neto and Zeileis 2010). Significance of effects of the tested variables and their interaction were assessed with an analysis of deviance using Chi-squared tests. Following Camphuysen (2013), a 3-parameter logistic growth curve was fitted to the body mass and total head length of each chick, from both field and aviary, approximating by least-squares the parameters of the logistic function:

$$y = \frac{a}{1 + be^{-kt}}$$

where y is the body mass or head length, a is the upper asymptote, b the body mass or head length at the point of inflection and k is the growth rate. The obtained upper asymptote and growth rate values were analysed by multiple regression with sex and the estimated proportion of terrestrial food in diet (field chicks) or diet treatment (aviary chicks), as well as their interactions, as explanatory variables. Significance of effects of the explanatory variables and their interactions were assessed by means of F-tests. A body condition index was calculated as the residual values of a linear regression of body mass on total head length (Reist 1985). Body condition index values were averaged per individual within each age period. These were analysed by means of linear mixed effects models, using R package nlme (Pinheiro et al. 2018), with sex, age period and the proportion of terrestrial food in diet (field chicks) or the diet treatment (aviary chicks), and all their possible two- and three-way interactions as explanatory variables. Chick identity was included as a random intercept.

Models were fitted using the Restricted Maximum Likelihood (REML) method to reduce bias in parameter estimations (Harville 1977). Model residual normality and homoscedasticity were assessed respectively by means of a Shapiro-Wilk normality test (Shapiro and Wilk 1965) and Breusch-Pagan test (Breusch and Pagan 1979). Significance levels of all performed tests were set at 5%. Only significant interactions were retained, while main effects were always retained to avoid parameter estimation bias (Whittingham et al. 2006).

Ethical approval

All applicable international, national, and institutional guidelines for the care and use of animals were followed during the aviary experiment (project EC number 2015-017) as well as in the field study (project EC number 2013-73). Additionally, all procedures performed in the aviary were in accordance with the regulations of the institution at which the studies were conducted (VOC Oostende).

Results

Variation in diet composition of field chicks

Estimated proportions of terrestrial food in the chick diet ranged from 4% to 67% (Fig. 1). The estimated proportions were skewed towards marine values (mean 18%, median 13% terrestrial component), implying that most field chicks were raised on a predominantly marine diet. The proportion of terrestrial food in the chick diet did not vary significantly in relation to chick age or sex (Table 1).

Effects of diet composition on chick development

Asymptotic body mass of both field and aviary chicks was significantly related to their diet composition (Table 2). In field chicks, asymptotic body mass was negatively related to the proportion of terrestrial food (Fig. 2a), while aviary chicks reached a higher body mass when raised on a terrestrial diet (Fig. 2b). Males attained a higher body mass than females in both field and aviary chicks, with similar effect sizes in both environments. Growth rates in field chicks (Fig.2c) did not vary with diet or sex. In contrast, aviary chicks gained body mass faster when raised on a terrestrial diet (Fig.2d). Male aviary chicks did not gain body mass significantly faster than females (Table 2).
Asymptotic head length of field chicks was inversely related to the proportion of terrestrial food in their diet, while male chicks attained a larger head length than females (Fig. 3a, Table 2). In aviary chicks, diet treatment had no effect on asymptotic head length, while males reached a higher value (Fig. 3b). Growth rates for head length in field chicks were not significantly related to the proportion of terrestrial food in their diet (Table 2). However, head length of male chicks grew at a higher rate than that of females (Fig. 3c). In aviary chicks, growth rates did not vary with diet or sex (Fig. 3d).

Effects of diet composition on body condition

For field chicks, the retained model contained an interaction between the proportion of terrestrial food in the diet and growth period (Table 3, Fig. 4a). During the first 10 days of growth, condition did not vary with the proportion of terrestrial food, while in the periods between 10 and 20, and 20 and 30 days after hatching, condition decreased with increasing proportion of terrestrial food. In aviary chicks, males showed a higher body condition than females (Fig. 4b), but no evidence was found for diet or age effects.

Discussion

Lesser Black-backed Gull chicks in the study colony of Zeebrugge showed a predominantly marine food signature. No cases of chicks fed solely on terrestrial food sources were detected, whereas an almost completely marine diet was frequent in our sample. Stable isotope signatures of individual chicks remained fairly constant throughout the rearing period, suggesting that the observed variation in diet composition was mainly due to consistent between-parent variation in feeding strategies, rather than temporary changes in food availability. Whereas a stronger terrestrial food signature corresponded with slower chick development under field conditions, no clear differences in chick development between terrestrial and marine diets occurred when food was provided *ad libitum* under controlled aviary conditions.

Higher trophic level diets, reflected by higher δ15N values (Ambrose and DeNiro 1986), have previously been linked to improved chick condition and higher breeding success in seabirds (e.g. Bukacinska et al. 1996; Janssen et al. 2011; Ronconi et al. 2014; Van Donk et al. 2017). Here, we did not find an intrinsic difference between marine and terrestrial diets when provided *ad libitum*. Instead, dietary effects on chick development only became apparent under field conditions, and may thus relate to differences in cost-benefit ratios between marine and terrestrial foraging strategies. High trophic fishery discards could therefore be assumed to constitute the most profitable food source when rearing chicks in Lesser Black-backed Gulls. However, foraging at sea is known to be highly competitive, and fishery discards are hence often only available to the largest birds, generally males (Camphuysen et al. 2015). Terrestrial food sources may thus be more frequently exploited by the less competitive individuals or during periods of marine food shortage (Navarro et al. 2010; Tew Kai et al. 2013; Tyson et al. 2015). This assumption is further supported by the fact that field chicks of both sexes raised on a predominantly marine diet attained larger body masses and head lengths, as well as a higher body condition from 10 days post-hatch onwards. Given that post-fledging survival rates in seabirds are positively related to fledgling size and condition (Lindström 1999; Stienen et al. 2002; Braasch et al. 2009; Bosman et al. 2016), a marine foraging strategy indeed appears most optimal in our coastal population. These results further imply that a more diverse diet, with both terrestrial and marine components, is less beneficial than a specialized marine diet. Similarly, Van Donk et al. (2017) found that higher dietary diversity did not lead to higher reproductive success in herring gulls.

However, the relationships between diet composition and chick development in free-ranging populations may be confounded by factors underlying the variation in the proportion of marine food delivered to chicks. These factors may include parental sex, age, experience, timing of breeding, synchronization between partners or environmental effects (e.g. Ramos et al. 2008; Camphuysen et al. 2015). Given that terrestrial food provided *ad libitum* appeared as suitable as marine food for raising chicks in a controlled aviary environment, differences in chick size and condition observed in the field might be due to differences in food quantity, rather than quality between diets. Indeed, if marine food is the preferred resource for chick provisioning, and lower-quality birds are outcompeted at sea and therefore forage more often on land, terrestrial diets may be associated with lower food provisioning rates. This hypothesis however relies on the assumption that the terrestrial diet provided to chicks raised in the aviary held no significant differences in quality with that provided to free-ranging chicks. Environmental factors potentially mediating the relationship between chick diet composition and chick development include variation in the relative availability of marine and terrestrial food sources, which can additionally affect the relative costs and benefits of different feeding strategies.

Integration of field sampling with aviary experiments in this study suggests that a terrestrial diet may lower reproductive success due to limitations in providing sufficient amounts of food to the chicks. This influences predictions on the effects of changes in marine food availability resulting from the announced reform of the Common Fisheries Policy (2008), which aims at ending the practice of discarding by 2019. Based on the predominantly marine signature of food provisioned to Lesser Black-backed Gull chicks in our study population, and the behavioural and reproductive responses to earlier sporadic cases of discard reduction in various Larus species (Oro et al. 1995; Chapdelaine and Rail 1997; Regehr and Montevecchi 1997; Camphuysen 2013; Tyson et al. 2015), it can be expected that the planned disappearance (or at least reduction) of fishery discards will affect breeding success in coastal breeding gulls. The impact of such discard ban may depend on the past history of the colony. For instance, the study colony at Zeebrugge was mainly founded by immigrants originating from nearby coastal colonies along the Southern North Sea that likely exploited fishery discards (Seys et al. 1998; Stienen et al. 2002), and can thus be expected to contain a large number of marine-specialist individuals. The extent to which local adaptation and social learning affect the cost of provisioning chicks with terrestrial food should be further assessed by studying the relationships here described in populations that are mostly reliant on terrestrial food sources (e.g. Coulson and Coulson 2008; Gyimesi et al. 2016), where specialists in different terrestrial foraging modes may be found. Moreover, early diet could affect an individual's proficiency at exploiting a particular foraging niche through ontogenetic effects on physiological and morphological traits (Oudman et al. 2016), further affecting the cost-to-benefit ratio of individual foraging strategies. Finally, more in-depth evaluation of fitness costs and benefits in early diets will require exploring the extent of differential investment of each member of a breeding couple, and integrating hidden costs such as contamination (Arcos et al. 2002; Jaspers et al. 2006; Santos et al. 2017).

Conclusions

Variation in the marine vs. terrestrial composition of the diet of free-ranging chicks, driven by differences in parental feeding strategies, resulted in impaired chick growth where a larger terrestrial component was found. Similar patterns do not arise when terrestrial and marine diets are provided *ad libitum* to hand-raised chicks. We suggest that anthropogenic terrestrial diets may lower reproductive success due to limitations in food quantity, rather than quality.

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Figure 1

Distribution of diet compositions inferred from field chick feather samples.

(a) Isospace for values of δ15N and δ13C in lesser black-backed gull feather samples relative to average (+/- SD) values of food sources. Stable isotope ratios in food sources are corrected using trophic enrichment factors. (b) Frequency histogram for the estimated proportion of terrestrial food in chick diet.

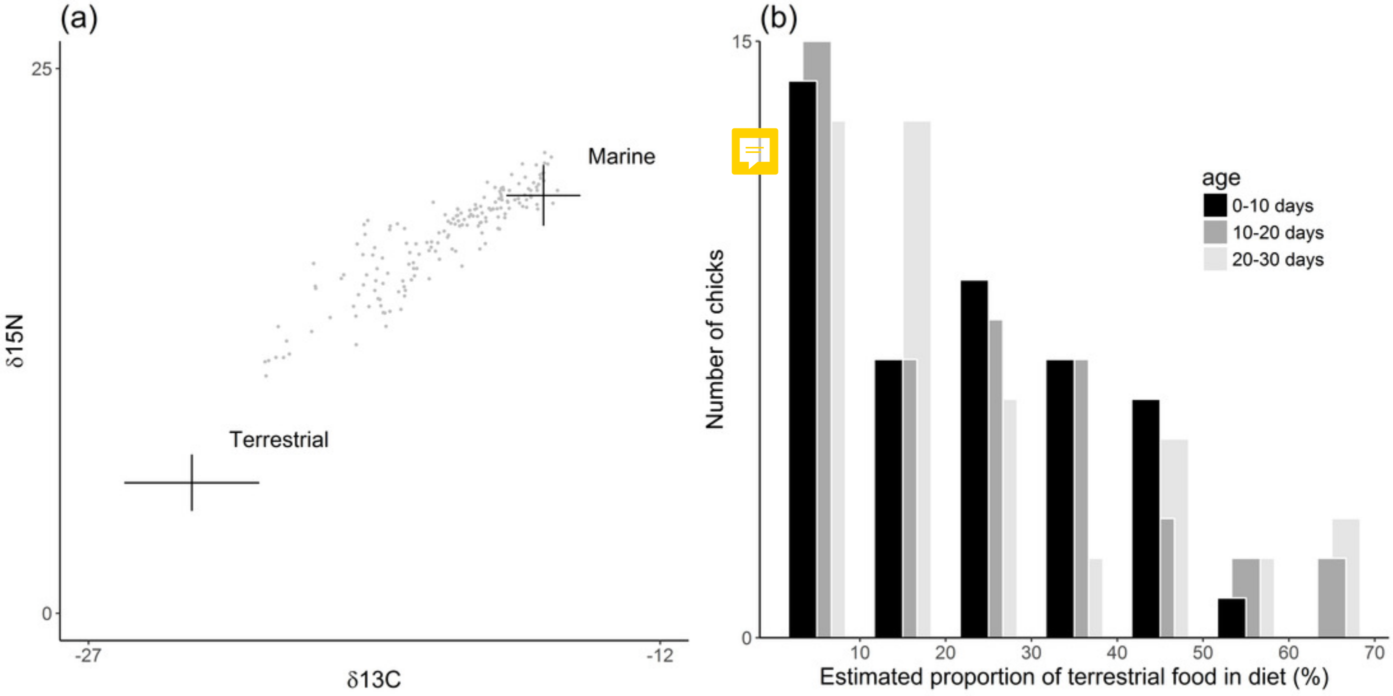

Figure 2

Asymptote and growth rate of body mass against diet composition.

(a) Estimated asymptotic body mass of male and female field chicks plotted against the estimated proportion of terrestrial food in the diet. Regression lines are plotted for significant relationships. (b) Box-plot of the asymptotic body mass in aviary chicks, per sex and dietary treatment. (c) Estimated growth rate plotted against the estimated proportion of terrestrial food in diet of field chicks, per sex. (d) Box-plot of the estimated growth rate of body mass in aviary chicks, per sex and treatment. Boxes correspond to median, first and third quartile, and whiskers to 1.5 times the interquartile range. ***: P<0.01

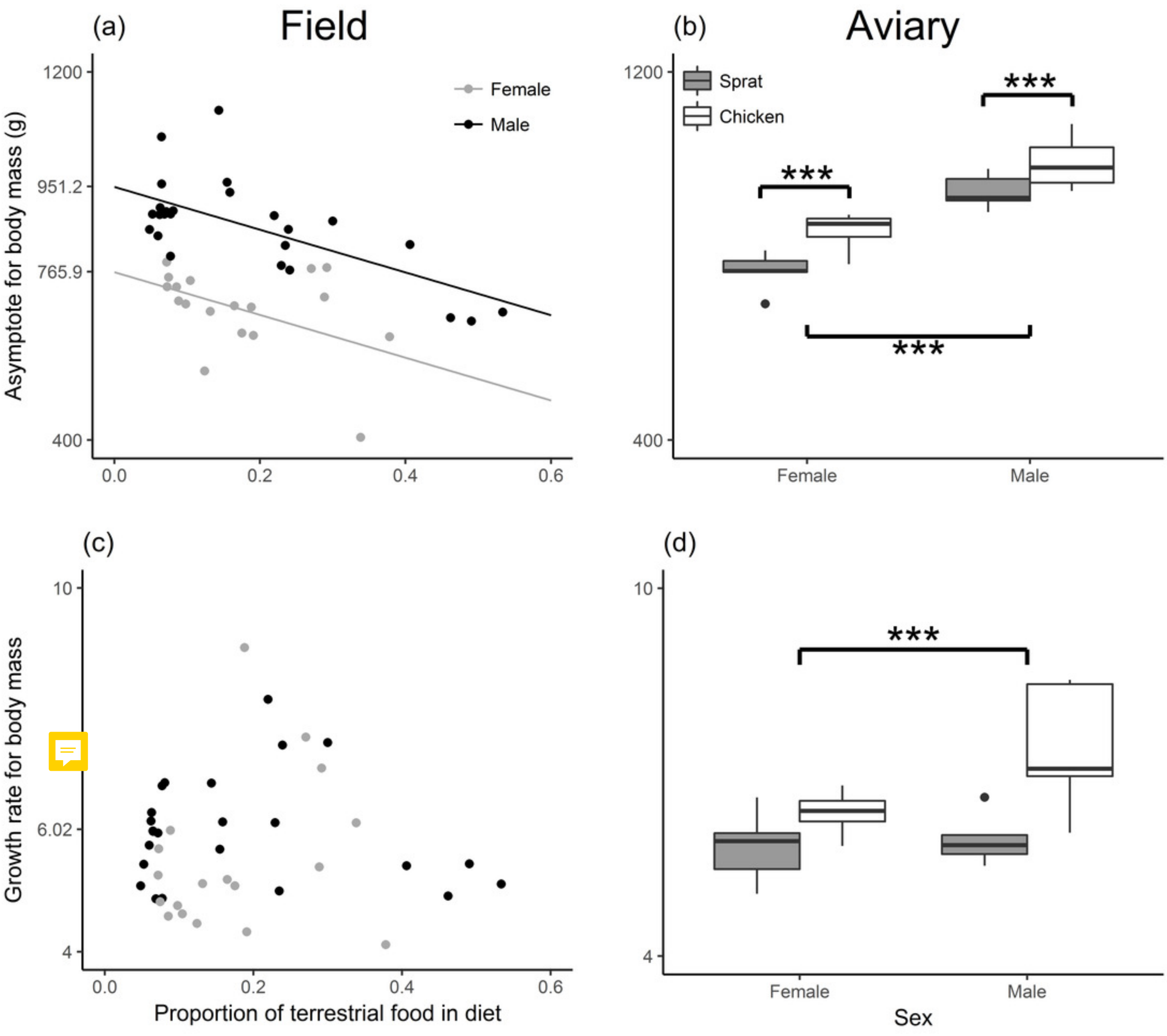
(a)
Field
Asymptote for body mass (g)
1200
951.2
765.9
400
0.0
0.2
0.4
0.6
Female
Male
(b)
Aviary
1200
400
Sprat
Chicken
***
***
***
Female
Male
(c)
Growth rate for body mass
10
6.02
4
0.0
0.2
0.4
0.6
Proportion of terrestrial food in diet
(d)
10
4
***
Female
Male
Sex

Figure 3

Asymptote and growth rate of head length against diet composition.

(a) Estimated asymptotic head length of male and female field chicks plotted against the estimated proportion of terrestrial food in the diet. Regression lines are plotted for significant relationships. (b) Box-plot of the asymptotic head length in aviary chicks, per sex and dietary treatment. ***: $p<0.01$ (c) Estimated growth rate plotted against the estimated proportion of terrestrial food in diet of field chicks, per sex. (d) Box-plot of the estimated growth rate of head length in aviary chicks, per sex and treatment. Boxes correspond to median, first and third quartile, and whiskers to 1.5 times the interquartile range.

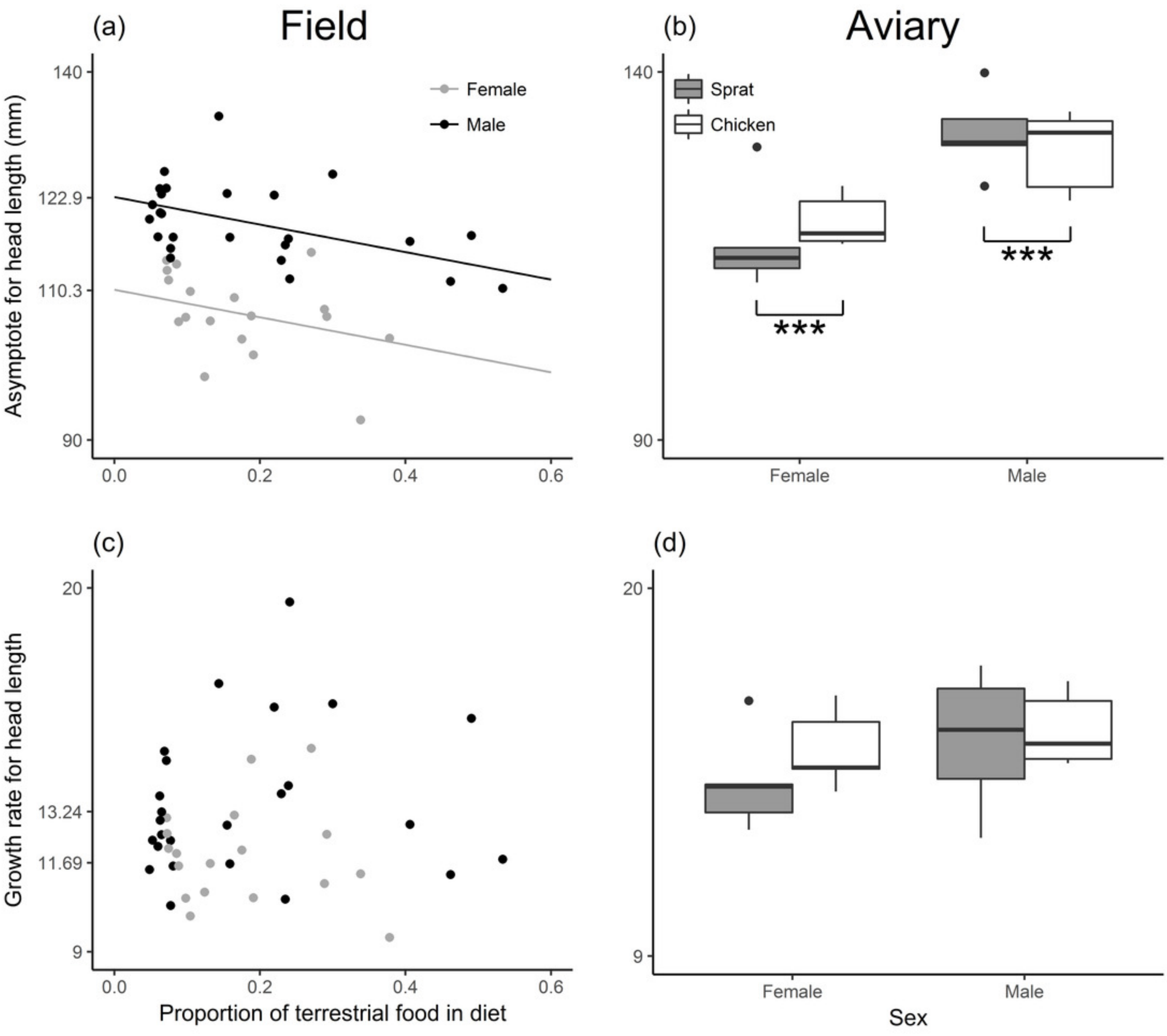
(a)
Field
(b)
Aviary
Asymptote for head length (mm)
140
122.9
110.3
90
Female
Male
Sprat
Chicken
***
***
0.0
0.2
0.4
0.6
Female
Male
(c)
(d)
Growth rate for head length
20
13.24
11.69
9
Proportion of terrestrial food in diet
Sex

Figure 4

Chick body condition index against diet composition.

(a) Condition index of male and female field chicks plotted against the estimated proportion of terrestrial food in the diet, per age category. Solid lines are plotted for instances where the relationship was found significant. (b) Box-plot of the condition index in aviary chicks, per sex, dietary treatment and age category. Boxes correspond to median, first and third quartile, and whiskers to 1.5 times the interquartile range. ***: P<0.01

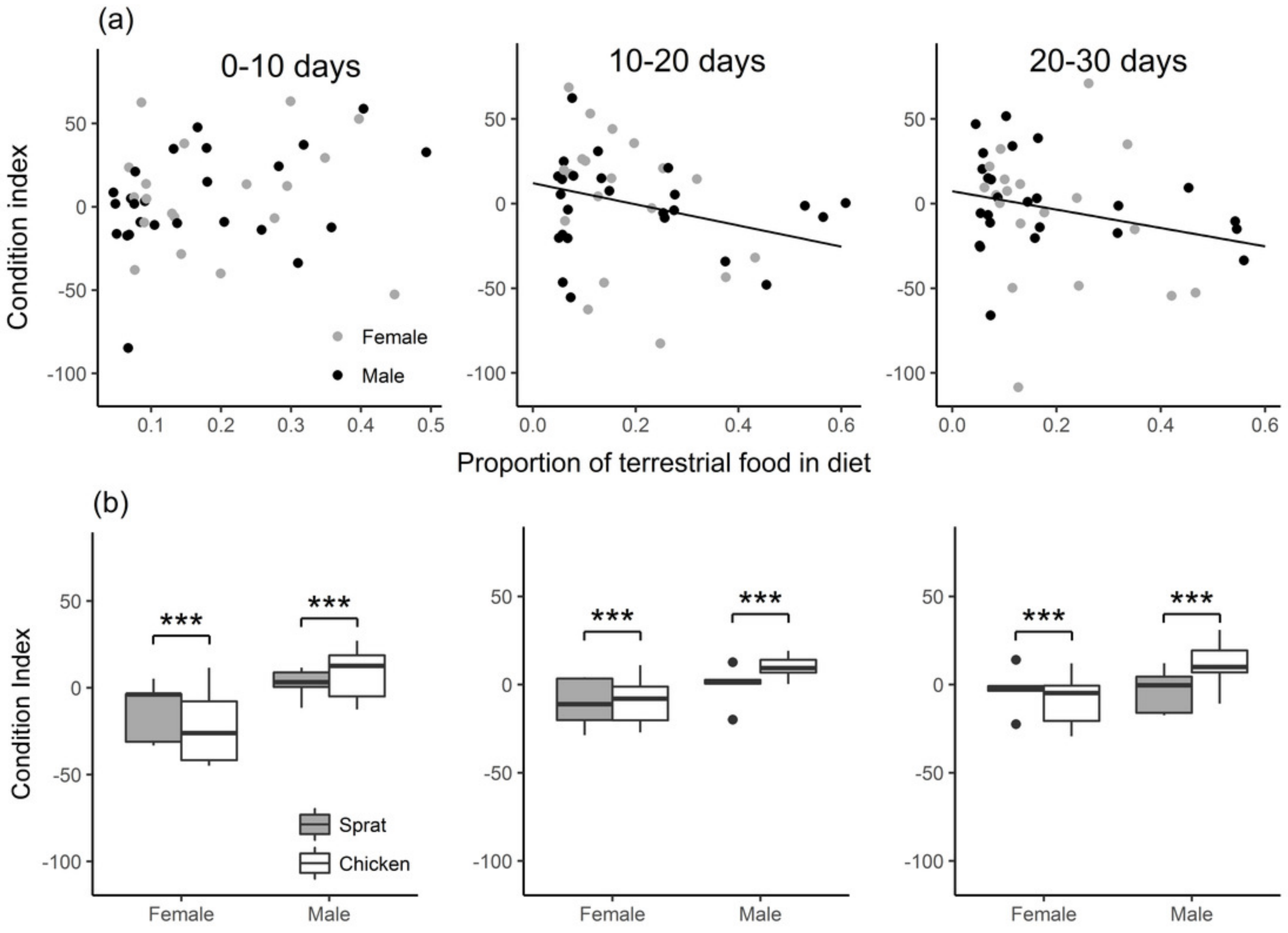

Table 1(on next page)

Beta regression model of the proportion of terrestrial food in diet of free ranging chicks in relation to sex and age period. The non-significant interaction between sex and age period was removed.

The non-significant interaction between sex and age period was removed.

	Estimated marginal mean ± s.e	**χ^2**	**d.f.**	**p-value**
Sex		0.64	1	0.42
Female	0.20 ± 0.02			
Male	0.18 ± 0.01			
Age		0.01	2	0.99
0-10 days	0.19 ± 0.02			
10-20 days	0.19 ± 0.02			
20-30 days	0.19 ± 0.02			

Table 2(on next page)

Multiple regression models of asymptotic size and growth rates of body mass and head length, in relation to sex and the proportion of terrestrial food in diet (field) or diet treatment (aviary).

Non-significant interactions were removed from each model.

	Parameter	Variable		Estimated marginal mean/coefficient ± s.e	F-statistic	d.f.	p-value
Body mass							
Field	Asymptote	Prop. Terr. food		-470.70 ± 93.72	22.78	1,40	<0.01
		Sex	Female	681.11 ± 21.15	50.52	1,40	<0.01
			Male	866.45 ± 15.23			
	Growth rate	Prop. Terr. Food		0.39 ± 1.51	0.10	1,40	0.75
		Sex	Female	5.51 ± 0.34	2.50	1,40	0.12
			Male	6.18 ± 0.25			
Aviary	Asymptote	Diet	Fish	852.85 ± 19.65	11.72	1,17	<0.01
			Chicken	947.98 ± 19.65			
		Sex	Female	809.41 ± 19.65	42.9	1,17	<0.01
			Male	991.42 ± 19.65			
	Growth rate	Diet	Fish	5.84 ± 0.22	10.60	1,17	<0.01
			Chicken	6.86 ± 0.22			
		Sex	Female	6.06 ± 0.22	3.52	1,17	0.08
			Male	6.64 ± 0.22			
Head length							
Field	Asymptote	Prop. Terr. food		-18.16 ± 5.82	8.11	1,40	<0.01
		Sex	Female	107.05 ± 1.31	60.50	1,40	<0.01
			Male	119.64 ± 0.95			
	Growth rate	Prop. Terr. Food		1.54 ± 2.36	0.42	1,40	0.52
		Sex	Female	11.93 ± 0.53	5.64	1,40	0.02
			Male	13.48 ± 0.38			
Aviary	Asymptote	Diet	Fish	124.38 ± 1.79	0.003	1,17	0.95

			Chicken	124.53 ± 1.79			
		Sex	Female	118.40 ± 1.79	22.88	1,17	<0.01
			Male	130.50 ± 1.79			
	Growth rate	Diet	Fish	14.82 ± 0.47	1.01	1,17	0.33
			Chicken	15.48 ± 0.47			
		Sex	Female	14.68 ± 0.47	1.99	1,17	0.18
			Male	15.61 ± 0.47			

Table 3(on next page)

Linear mixed effects models of the body condition index of free-ranging (field) and aviary chicks in relation to sex and the proportion of terrestrial food in diet (field) or diet treatment (aviary).

Non-significant interactions were removed from each model. *: $p<0.05$.

	Estimated marginal mean/ coefficient ± s.e	F-statistic	d.f.	p-value
Field				
Proportion Terr. Food		1.97	1,83	0.16
Sex		0.004	1,42	0.95
Female	0.90 ± 5.15			
Male	1.29 ± 4.81			
Age		0.98	2,83	0.38
0-10 days	5.60 ± 4.96			
10-20 days	0.84 ± 4.96			
20-30 days	-3.16 ± 4.96			
Prop. Terr. Food x Age		3.56	2,83	0.03
0-10 days	52.89 ± 40.07			
10-20 days	-118.37 ± 46.89*			
20-30 days	-105.16 ± 47.57*			
Aviary				
Diet		0.33	1,17	0.57
Fish	-4.70 ± 3.72			
Chicken	-1.67 ± 3.72			
Sex		8.95	1,17	<0.01
Female	-11.05 ± 3.72			
Male	4.68 ± 3.72			
Age		0.1	2,38	0.38
0 – 10 days	-6.06 ± 3.39			
10 – 20 days	-2.55 ± 3.39			

20 – 30 days	-0.95 ± 3.39			

2