



RESEARCH ARTICLE

Coupling bio-logging with nutritional geometry to reveal novel insights into the foraging behaviour of a plunge-diving marine predator

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ABSTRACT

It is widely believed that predators maximise their energy intake while foraging and consume prey that are nutritionally similar. We combined GPS data loggers, miniaturised cameras, dietary sampling and nutritional geometry to examine the nutritional variability in the prey and selected diet, and foraging performance, of the masked booby (*Sula dactylatra tasmani*), a wild carnivore and marine top predator. Data loggers also revealed no significant differences between sexes in the foraging performance of chick-rearing adults. Females provided more food to their chicks than the males and, regardless of the nutritional variability of prey consumed, both sexes showed similar amounts of protein and lipid in their diets. Miniaturised cameras combined with nutritional analysis of prey provided, **for the first time**, fine-scale detail of the amounts of macronutrients consumed in each plunge dive and the overall foraging trip. Our methodology could be considered for future studies that aim to contribute to the general understanding of the behavioural and physiological mechanisms and ecological and evolutionary significance of animal foraging (e.g. energy expenditure budgets and prey selection for self- and offspring-feeding that could lead to sex-specific foraging strategies).

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Introduction

Predators play an important role in the structure and function of food webs and ecological communities (Paine 1980). It is widely believed that predators feed on foods that are nutritionally similar, suggesting that quantity drives their selection (Westoby 1978; Stephens & Krebs 1986). The recent development of a multidimensional geometric framework known as nutritional geometry (NG) has simplified the complexities of modelling foods in

relation to foraging behaviour, the type of predator, geographic location and social interactions, providing a novel ecological view of nutrition (Raubenheimer et al. 2009; Simpson & Raubenheimer 2012). NG enables scientists to unravel the importance of food quality in relation to macronutrient (protein, lipid, carbohydrate) ratios in a wide range of taxa in the laboratory and a few herbivores and omnivores in the wild (reviewed in Simpson & Raubenheimer 2012). NG includes two different modelling approaches: amounts-based (AB); and right-angled mixture triangle (RMT). The former requires the accurate collection of foods consumed and has been applied extensively in laboratory studies, whereas the latter is a proportional model that has been broadly applicable to field studies (Raubenheimer 2011). Field-based research has the challenge to overcome complex logistical constraints to collect reliable data for nutritional studies in both aquatic (reviewed in Tait et al. 2014) and terrestrial environments (reviewed in Raubenheimer et al. 2015).

One of the main challenges in studying the nutritional ecology of animals in the wild is undertaking the prolonged observations necessary to interpret foraging behaviour and food intake. Only a few species have been able to habituate to human presence sufficiently to allow observation of their foraging behaviour in the field (e.g. Goodall 1964; Whiten et al. 1999; Rothman et al. 2011). AB nutritional models have, to date, been successfully applied in three field projects: Peruvian spider monkeys, *Ateles chamek* (Felton et al. 2009); mountain gorillas, *Gorilla beringei beringei* (Rothman et al. 2011); and chacma baboons, *Papio hamadryas ursinus* (Johnson et al. 2013). All involved primates that were able to habituate to human presence, thereby facilitating accurate behavioural observations (Raubenheimer et al. 2015). However, the vast majority of animals are highly evasive and difficult to observe in the wild for extended periods. Adding to this challenge, marine predators generally spend most of their lives at sea. As a consequence, studies involving direct observations on foraging behaviour of marine predators are rare.

Bio-logging technologies have made significant contributions to understanding how predators utilise three-dimensional spaces while foraging (reviewed in Wilson et al. 2002; Ropert-Coudert & Wilson 2005; Ropert-Coudert et al. 2009). Miniaturised data loggers have been deployed on unhabituated free-ranging species, in particular seabirds, providing researchers the ability to collect fine-scale detail of global positioning, acceleration and surrounding abiotic factors that can be modelled to profile 3D environments (Grémillet et al. 2004; Machovsky-Capuska et al. 2013). The recent expansion of bio-logging using miniaturised cameras enables the collection of visual information from the animals' perspective (Moll et al. 2007).

Deployments of miniaturised cameras have provided the ability to unravel at-sea behaviours of marine predators including diving tactics and prey capture success (Davis et al. 1999; Watanabe et al. 2006; Takahashi et al. 2008; Heaslip et al. 2012), social interactions (Sakamoto et al. 2009; Yoda et al. 2011), and interactions with their environment and fisheries (Grémillet et al. 2010; Votier et al. 2013; Tremblay et al. 2014). None, however, have been able to capture high-resolution footage on foraging decisions over an entire foraging trip.

The hitherto unrealised coupling of bio-logging technology with NG could yield powerful insights into carnivore foraging strategies and nutritional ecology. Here, we combine GPS data loggers, miniaturised cameras, diet analysis and NG to examine the nutritional variability in the prey and selected diet, combined with foraging performance, of a wild carnivore and marine top predator, the masked booby (*Sula dactylatra tasmani*). Masked boobies are large (weight 2.4–2.9 kg) members of the Sulidae family (gannets and boobies) which are

classified as **Near Threatened** (Garnett et al. 2011). These marine predators alternate short and long foraging trips that enable them to balance self- and offspring-feeding (Sommerfeld et al. 2013a). Foraging investment plays an important role in the division of labour in biparental care systems (Bijleveld & Mullers 2009). Species that show reverse sexual dimorphism (RSD), where females are larger than males, are known for having sex-specific foraging differences (reviewed in Lewis et al. 2002). We seek to gain a better understanding of the nutritional ecology of this species, addressing three questions: **1.** Does macronutrient composition vary between prey species? **2.** Do masked boobies show sex-specific foraging strategies (in terms of foraging behaviour and macronutrient consumption)? **3.** Can bio-logging be coupled with NG to provide fine-scale detail of the amounts of macronutrients consumed in each plunge dive and the overall foraging trip? We also discuss future directions in field-based nutritional ecology using bio-logging science.

Materials and methods

Study area

The study was conducted in September 2013 at Muttonbird Point, Lord Howe Island, Australia (31°30' S, 159°04' E). The masked booby population on Muttonbird Point is estimated at c. 200 breeding pairs (Priddel et al. 2005).

Data logger deployment

Ten chick-rearing adults (chicks 2–5 weeks old) were captured with a blunt-tip shepherd's crook at their nests and sexed by differences in pitched voice (Nelson 1978). We used two types of loggers (continuous GPS—1 s intervals—and a continuous recording camera) which were attached with Temflex 1610 tape to the four central tail feathers. Five males and three females were equipped with GPS data loggers weighing 45 g each (manufactured by e-obs digital telemetry in Germany; see more details in Machovsky-Capuska et al. 2013) and two males were fitted with customised miniature video cameras (U10 AU USB Flash Drive DVR Camera DV, Figure 1A). The cameras deployed had a 36° lens angle and sensor resolution of 720 × 480 HD at 30 frames per second with a MicroSD 64 GB storage capability. The unit was powered by a 3400 mAh lithium polymer battery that enabled 19 h of continuous video recording. All components were encapsulated in waterproof housing for immersion to depths of 20 m. The total package was 60 × 60 × 15 mm (L x W x H) and weighed 70 g, which is below the 3% threshold (the weight of logger in relation to the adult body mass) beyond which behavioural disruptions are likely to occur in flying seabirds (Vandenabeele et al. 2014). To aid rapid identification, each bird was uniquely marked on the chest with permanent non-toxic ink as in Machovsky-Capuska et al. (2014). Marked birds were recaptured upon arrival at the colony after foraging, and the loggers retrieved.

Foraging performance

The high resolution detail of the miniaturised cameras allowed us to estimate parameters of foraging performance that were used to interpret information from the continuous GPS data loggers. We defined the duration of a foraging phase (FP) as the time interval

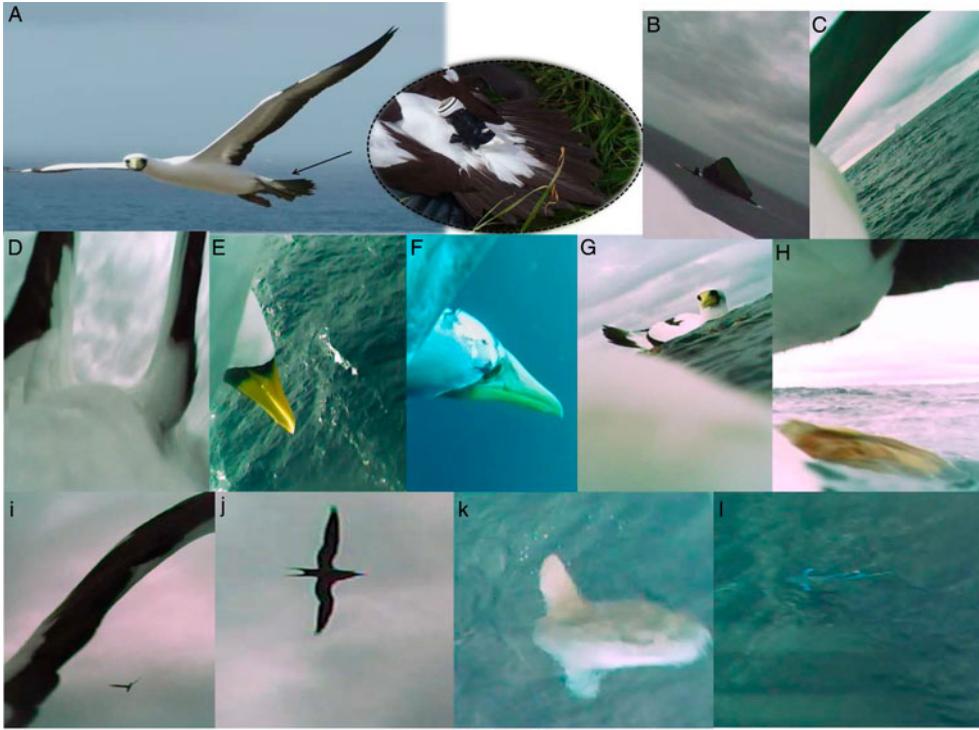
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Figure 1 Digital still images obtained from bird-borne camera attached to two male chick-rearing adult masked boobies. **A**, Flying bird with a miniaturised camera attached to the four central feathers of the tail; **B**, bird heading NE away from Muttonbird Point for a splash down during a short trip (within 1.5 km from the colony); **C**, foraging bird returning to the colony (at least 55 km away) at dusk approaching from the SSW from S of Balls Pyramid; **D–H**, a foraging phase (FP) that consists of ascent: **E**—aerial phase of the plunge dive: **F**— underwater phase of the plunge dive: **G**—resting near a conspecific: **H**—take off; **I**, foraging in the presence of conspecifics; **J**, frigate bird in association with camera-mounted bird; **K**, plunge diving in the presence of sunfish (*Mola mola*); **L**, aerial prey detection of flying fish (Exocoetidae).

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encompassing the ascent, plunge dive (aerial and underwater phases), subsequent resting on the water and take off (Weimerskirch et al. 2005). Based on the video footage collected we established a mean dive duration of 5.8 s that allowed us to infer diving behaviour from the interruptions of continuous GPS signals following Machovsky-Capuska et al. (2013). Video footage was analysed frame by frame using Avidemux 2.6.4.

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Following Grémillet et al. (2004), maximum distance away from the colony (MDC), total foraging path (TFP), foraging trip duration (FTD), flying time (FT), resting time (RT) and total dive duration (TDD) were estimated from the recorded GPS data. Following Sommerfeld et al. (2013b), we established short and long foraging trips depending on their duration and the presence of plunge-diving events.

Prey composition of diet

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Dietary samples were collected in separate polythene bags from boobies that regurgitated during handling (Priddel et al. 2005). Prey obtained from the regurgitations were

individually weighed to 0.1 g, total length measured to 0.1 cm and identified to the lowest possible taxonomic level using published guides (Allen 2009). To evaluate prey preferences differences between females and males, we used binomial generalised linear models (GLMs; Bolker et al. 2009).

To estimate the macronutrient variation of prey species and calculate the nutritional composition of the boobies' diet, undigested samples of prey were selected from the regurgitations for proximate composition analysis (total lipid, nitrogen, moisture and ash). The most representative prey samples selected include flying fish (*Cheilopgon* spp., $n = 4$), yellow tail kingfish (*Seriola lalandi*, $n = 2$) and mackerel scad (*Decapterus macarellus*, $n = 2$). All prey samples were frozen within 5 h of collection and stored at -20°C . Proximate composition analysis of the different prey species was conducted following Tait et al. (2014). In accordance with Raubenheimer (2011), we plotted RMTs to show the proportional macronutrient variation (protein, lipid and rest—the sum of moisture and organic matter) in the prey consumed by masked boobies and also the nutritional composition of their diet as a result of mixing multiple foods. Following Raubenheimer & Rothman (2013), macronutrient masses were converted to energy (E) using standard conversion factors (protein = 17 Kj/g and lipid = 37 Kj/g). We randomly permuted intake of protein, lipid, rest and energy between sexes 100,000 times to evaluate the probability that the observed distribution would occur randomly and thus corrected for biases due to small sample size. Following Raubenheimer & Simpson (1997) we calculated in two steps the macronutrient intake of a foraging trip using AB models: step 1, we multiplied the macronutrient composition of each prey (g) by the number of prey ingested at each plunge dive; step 2, we summed the macronutrient consumption of all plunge dives (as explained in step 1) to obtain the macronutrient intake for each foraging trip. The balance of nutrients of the prey consumed in each foraging trip was connected using a line (also called 'nutritional rail') that passes through the origin of the graph and through each point that represents the quantity of the prey type.

Macronutrient intake and foraging performance

To combine foraging performance analyses with estimates of macronutrient intake we used only dietary samples collected upon data logger retrieval. Masked boobies feed mainly by plunge-diving from the air into the water (Weimerskirch et al. 2008) and for an accurate representation of the macronutrient intake in relation to foraging activity we used only trips in which plunge-diving was established. Following Machovsky-Capuska et al. (2011), we use the total dive duration per foraging trip to calculate the overall diving efficiency in regards to total meal size, grams of protein (P), lipid (L) and rest ($100\% - [P + L]$) consumed.

Due to small sample size, data from GPS loggers and cameras were initially tested using Levene's test for homoscedasticity and Shapiro-Wilk's test for normality and t -test for subsequent comparisons. Foraging phases, foraging trip duration and diving efficiency data (used as a continuous variable) were log₁₀ transformed and statistically tested using t -tests. All data were analysed using the statistical program PASW Statistics 19 (IBM Corp, Somers). Results are presented as mean \pm standard deviation (SD). This study was conducted under Office of Environment and Heritage (NSW) Animal Ethics permit OEH 021028/02.

Results

Miniaturised cameras

Video footage collected from two male chick-rearing masked boobies showed a total of six foraging trips. Using known landmarks (e.g. Figure 1B) we estimated that short trips extended at least 1.5 km from the colony and long trips at least 55 km from the colony (Figure 1C–D). A fine-scale detailed analysis of the footage revealed two FPs in six trips (33.0%, Figure 1E–I). The two trips with a FP (3.6 ± 1.8 h) were longer than those without foraging activity (0.3 ± 0.1 h) ($t = -4.91$, d.f. = 4, $P < 0.05$; for more details see Table 1). Of a total of 14 plunge dives recorded (TDD, 5.8 ± 0.5 s), six were in the presence of sunfish. Plunge dive duration (6.7 ± 0.7 s) was longer in the presence of sunfish than in their absence (4.7 ± 1.5 s) ($t = -2.28$, d.f. = 12, $P < 0.05$). Boobies foraged in the presence of conspecifics (Figure 1I), frigatebirds (Fregatidae; Figure 1J) and sunfish (*Mola mola*; Figure 1K), and preyed upon flying fish (Exocoetidae, Figure 1L).

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GPS data loggers

We successfully collected a total of 24 single-day foraging trips from eight individual birds. All the individual foragers showed a combination of two short and one long foraging trip. Masked boobies spent 3.0 ± 3.7 h during their foraging trips, an average MDC of 30.6 ± 37.0 km and TFP of 104.0 ± 130.2 km. Following our analyses with miniaturised cameras, only the longer trips showed plunge-diving behaviour (33.0%, Table 1), and we collected a total to 229 dives. No significant differences between cameras and GPS loggers were observed in the FTD (5.4 ± 0.4 h and 3.7 ± 1.5 h, respectively; $t = -1.35$, d.f. = 6, $P = 0.22$) and TDD (35.7 ± 9.2 s and 29.8 ± 9.5 s, respectively; $t = 1.69$, d.f. = 6, $P = 0.14$) (Table 1). Combining GPS and camera data, masked boobies spent on average 75.7% ($\pm 11.6\%$) of the time flying, 24.0% ($\pm 11.7\%$) resting on the water and less than 0.5% of the time plunge-diving. No significant differences were observed between females and males in the MDC (67.4 ± 36.8 km and 38.5 ± 29.4 km, respectively; $t = -1.06$, d.f. = 4, $P = 0.35$), TFP (182.3 ± 80.1 km and 153.4 ± 123.8 km, respectively; $t = -0.34$, d.f. = 4, $P = 0.75$), FTD (4.0 ± 1.1 h and 4.2 ± 1.9 h, respectively; $t = 0.19$, d.f. = 6, $P = 0.85$) and TDD (29.5 ± 14.3 s and 30.0 ± 8.5 s, respectively; $t = 0.07$, d.f. = 6, $P = 0.95$).

Table 1 Performance of foraging and macronutrient intake in chick-rearing adult masked boobies at Muttonbird Point (Lord Howe Island, Australia) in 2013.

Bird	Sex	Logger	MDC (km)	TFP (km)	FTD (h)	TDD (s)	P (g)	L (g)	R (g)	P:L ratio	Total (KJ/g)
B1	M	GPS	26.7	118.5	3.1	26.3	39.3	4.8	63.2	8.2	1671.7
B2	F	GPS	51.0	125.9	3.2	46.0	94.3	5.0	349.8	18.9	6679.9
B5	M	Camera	–	–	5.0	44.9	68.9	2.8	252.3	24.6	4802.2
B6	M	GPS	16.8	50.8	1.4	28.3	52.5	3.0	194.6	17.5	3724.5
B9	M	Camera	–	–	5.8	26.5	54.5	2.6	199.3	21.3	3807.6
B15	F	GPS	41.7	147.0	3.5	21.0	62.2	3.0	231.0	21.0	4398.6
B24	F	GPS	109.6	274.0	5.3	21.4	96.3	4.6	362.0	20.8	6874.1
B25	M	GPS	71.9	291.0	5.9	24.0	37.2	1.8	136.2	21.2	2601.7

FTD, foraging trip duration; MDC, maximum distance away from the colony; L, lipid; P, protein; P:L, protein:lipid ratio; R, rest; TDD, total dive duration; TFP, total foraging path.

Prey composition of diets

Eleven regurgitations were collected from different individuals. The mean mass of prey per regurgitation was 297.0 ± 99.4 g, which represented between 10.2% and 12.4% of the range of adults' body weight. The 25 prey items identified from these samples were all fish. Half of the regurgitations contained one prey species while the other half contained from two to five prey species, showing that masked boobies are able to feed on mixed diets. By mass, flying fish was the most representative prey (72.0%), followed by yellow tail kingfish (18.1%) and mackerel scad (9.9%). Fish collected from regurgitations had an average mass of 126.3 ± 123.7 g and had an average total length of 23.9 ± 10.4 cm.

Females (361.0 ± 86.9 g, $n = 5$) brought to the colony bigger meals than males (243.6 ± 50.5 g, $n = 6$, $t = 2.18$, d.f. = 9, $P < 0.05$). We found no significant differences between sexes in prey preferences (binomial GLZM: Wald test, $z = 1.76$, d.f. = 1, $p = 0.18$). There were no significant differences between the sexes in the length ($t = -1.61$, d.f. = 23, $P = 0.12$), weight ($t = -1.18$, d.f. = 23, $P = 0.25$) or number ($t = -0.84$, d.f. = 9, $P = 0.43$) of the individual fish brought to the colony.

Macronutrient composition of prey, diets and dietary intake

The RMT shows that the protein-to-lipid ratio (P:L) from the different foods consumed by masked boobies varied considerably, from 2.8:1 (yellow tail kingfish), 7.4:1 (mackerel scad) to 25.0:1 (flying fish) (Figure 2). In addition, we estimated the macronutrient composition of the diet aggregated across all individuals sampled to be 20.9:1.8:77.3 (P:L:R), with a P:L ratio of 11.6:1 (Figure 2).

No significant differences between males and females were observed in the absolute intake of protein (males, $n = 6$, 54.2 ± 14.8 g and females, $n = 5$, 75.6 ± 18.1 g, $t = 2.17$, d.f. = 9, $P = 0.08$), lipid (males, $n = 6$, 3.1 ± 1.0 g and females, $n = 5$, 4.3 ± 1.2 g, $t = 1.66$, d.f. = 9, $P = 0.13$) or rest (males, $n = 6$, 186.2 ± 76.9 g and females, $n = 5$, 281.1 ± 68.5 g, $t = 2.14$, d.f. = 9, $P = 0.08$), nor in the overall energetic consumption (males, $n = 6$, 3631.8 ± 1320.6 kJ/g and females, $n = 5$, 5375.6 ± 1281.5 kJ/g, $t = 2.14$, d.f. = 9, $P = 0.08$). Due to small sample size, the absolute intake of protein, lipid, rest and energy was tested using 100,000 permutations (see Materials and methods) and were not significantly less than expected by chance ($P > 0.05$).

Macronutrient intake and foraging performance

From the eight chick-rearing adult masked boobies carrying loggers (three females and five males), we established foraging performance in relation to macronutrient intake (Table 1). The overall cost of macronutrient gains in relation to foraging trip duration was 19.9 ± 14.1 g/h (protein) and 0.9 ± 0.6 g/h (lipid), whereas the cost of macronutrient gains in relation to foraging path was 0.6 ± 0.4 g/km (protein) and 0.2 ± 0.02 g/km (lipid). No significant differences between sexes were observed in foraging (females 104.2 ± 25.6 g/h and males 88.4 ± 55.5 g/h, $t = -0.19$, d.f. = 6, $P = 0.86$) or diving performance in relation to meal size (females 19.6 ± 4.2 g/s and males 14.6 ± 7.4 g/s, $t = 1.32$, d.f. = 6, $P = 0.24$), protein (females 65.2 ± 24.2 g/s and males 61.9 ± 18.7 g/s, $t = 1.50$, d.f. = 6, $P = 0.18$), lipid (females 3.1 ± 1.2 g/s and males 3.6 ± 1.0 g/s, $t = 1.13$, d.f. = 6, $P = 0.30$) and rest (females 243.1 ± 92.5 g/s and males 211.8 ± 93.0 g/s, $t = 1.28$, d.f. = 6, $P = 0.25$).

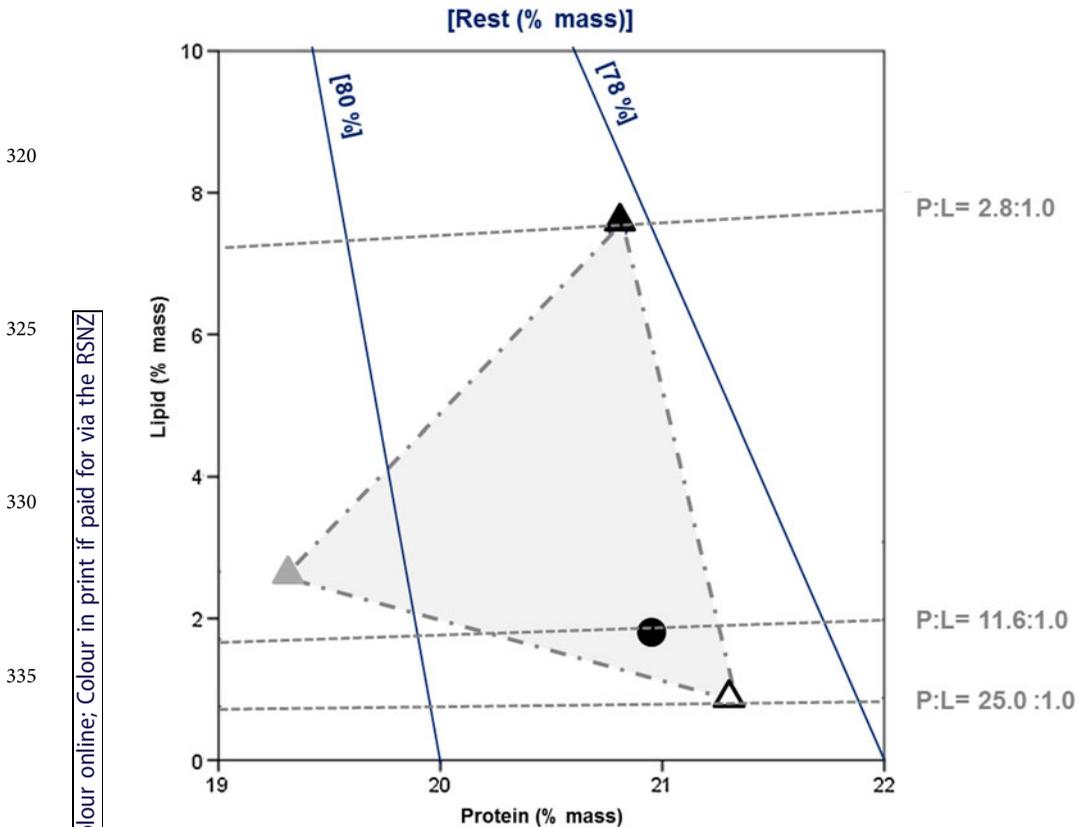


Figure 2 Right-angled mixture triangles (RMT) provide a means to visualise and compare proportional relationships of three mixture components (here protein [P], lipid [L] and rest [$R = 100\% - (P + L)$]) in two dimensional graphs. The triangles are the most representative prey species consumed by masked boobies. Flying fish (Δ) which comprises 21.3% P, 0.9% L and 77.9% R. Yellow tail kingfish (\blacktriangle) which comprises 20.8% P, 7.5% L and 71.7% R. Mackerel scad (\blacktriangle) which comprises 19.3% P, 2.6% L and 78.1% R. The resulting diet (\bullet) is composed of 20.9% P, 1.8% L and 77.3% R and is constrained to lie within the short dashed and dotted grey triangle connecting these foods (also known as 'nutritional niche').

Miniaturised cameras allowed us to establish prey detection and capture success of flying fish (both birds) during their overall foraging trips. Bird five (B5) consumed five fish over eight plunge dives recorded (62% capture success), whereas bird nine (B9) captured three fish over six plunge dives (50% capture success). AB model shows that B5 consumed more grams of lipids (L), protein (P) and energy (E) ($L = 2.68$ g, $P = 68.80$ g, $E = 4802.2$ Kj/g) than B9 ($L = 2.24$ g, $P = 54.23$ g, $E = 3807.6$ Kj/g) during their overall foraging trips (Table 1). However, both birds consumed similar P:L ratios in their diets ($B5 = 25:1$ and $B9 = 24:1$; Figure 3).

Discussion and conclusions

Understanding the relationships between nutrition, behaviour, ecology, morphology and physiology is a central aim in nutritional ecology (Raubenheimer et al. 2009). There are multiple challenges that have prevented translating nutritional ecology from the laboratory to

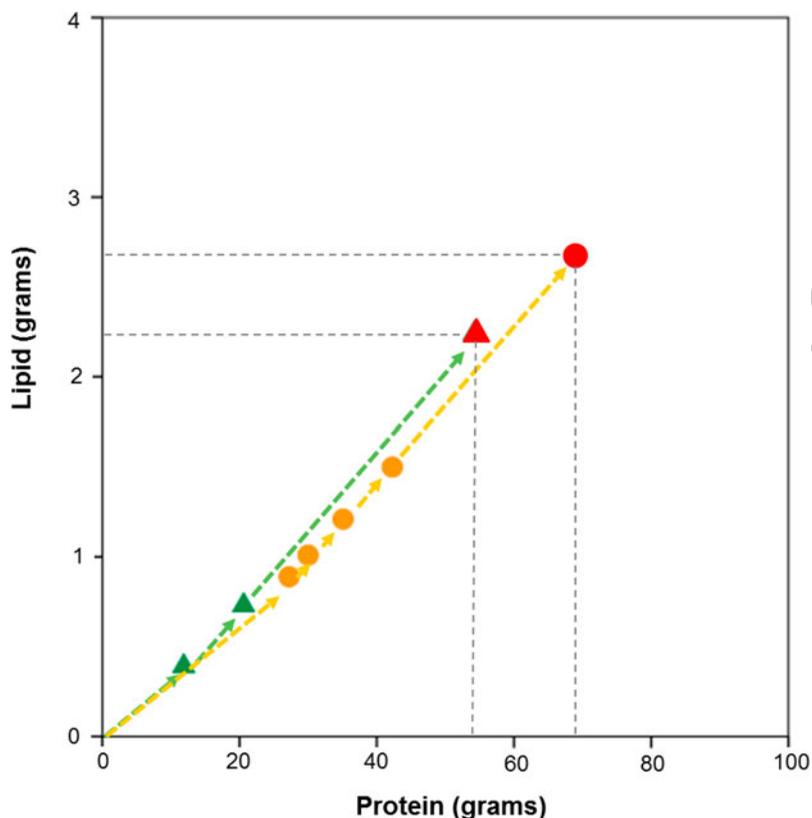


Figure 3 Miniaturised cameras deployed on the central tail feathers of two male chick-rearing masked boobies coupled with amount-based models (AB) allowed us to establish the macronutrient intake for a foraging trip. First, we established the macronutrient composition of each individual flying fish captured. Second, we multiplied the nutritional composition of each prey (g) by the number of prey ingested at each plunge dive (represented by [green] triangles and [golden] circles). Third, we summed the macronutrient consumption of all plunge dives (as explained in step 2) to obtain the macronutrient intake for each foraging trip (represented by a [red] triangle and a [red] circle). The balance of nutrients of the prey consumed in each foraging trip was connected connected by arrows (that represent each individual's nutritional rails). Circle = bird five; triangle = bird nine (see Table 1 for more details).

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the field to answer ecological questions related to nutrition in predators including difficulties in: **understanding** foraging behaviour of inaccessible and/or dangerous wildlife; collecting accurate estimations of food consumption; and **collecting** prey consumed for proximate composition analysis within a similar spatiotemporal scale (Tait et al. 2014; Raubenheimer et al. 2015). To the best of our knowledge, the present study is the first to overcome these challenges to examine the nutritional ecology of a marine predator, the masked booby, by using bio-logging science to collect data that can be analysed using **NG**.

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Foraging behaviour

Weimerskirch et al. (2007, 2008, 2009) and Sommerfeld et al. (2015) suggested the combination of short and long trips displayed by some seabirds, including masked boobies,

were part of a bimodal foraging strategy. However, our findings show that during short trips (within 1 h) masked boobies only rest on the water and do not forage; foraging occurs only during long trips (over several hours) and may include several FPs. Although, the interpretation of this result is subject to the caveat of our small sample size, the detection of false areas of restricted search (ARS) and diving zones can occur during short trips in proximity to the colony providing misleading information on the identification of real feeding areas (Sommerfeld et al. 2013b). It has been suggested that the identification of ARS behaviour is crucial to understand foraging movements and diving tactics in marine predators (Weimerskirch et al. 2007; Sommerfeld et al. 2013a). Our results demonstrate that masked boobies use FPs with up to three consecutive plunge dives when food patches were discovered. FPs often took place in the presence of sunfish, which are well known to compete with flying fish for copepods (Parin 1968). In the presence of predators, copepods are likely to elicit an escape response by descending into the water column thereby forcing schools of flying fish to dive deeper (Lewis et al. 1962). It has been suggested that plunge divers alter their dive duration in relation to the depth of the prey (Machovsky-Capuska et al. 2011). This could be the likely scenario for the increment observed in the duration of the ascent phase to higher altitudes and the extended duration of the plunge dives in order to increase prey capture success in the presence of sunfish.

While RSD is rare in seabirds, high sexual size dimorphism is characteristic of booby species (*Sula* spp., Nelson 1978). Within this group, larger females can easily buffer periods of food stress, increasing their ability to forage over longer distances and therefore different habitats (Weimerskirch et al. 2006). Miniaturised cameras and GPS loggers revealed no significant differences between sexes in the foraging performance of the masked boobies we studied, consistent with previous findings for the same species by Sommerfeld et al. (2013a); on the other hand, such differences might be detected using larger sample sizes.

Food consumption and macronutrient composition

Offspring rearing is considered to be the period of highest energy demand for adult seabird parents (Ricklefs 1983). A successful marine predator requires complex foraging strategies that enable them to balance self- and offspring-maintenance (Machovsky-Capuska et al. 2014). Our results show that boobies only captured prey during the long trips (up to 6 h) and spent up to 1.5 h of the time resting in the water. Fish digestion in seabirds has been suggested to take approximately 2 to 6 h depending on the prey (Davis 1956), and it is likely that boobies were self-feeding during the first part of the trip before then capturing prey for their chicks, as previously found in gannets (*Morus* spp., Hamer et al. 2000). Therefore, the food collected in the regurgitations at the colony could be considered to cover the chicks' nutritional demands.

Larger female masked boobies are suggested to be the main provisioners of food for their chicks, covering most of their energetic and nutritional demands (Weimerskirch et al. 2009). Our results showed that females brought more grams of food than males in diets similarly composed of mixed species (flying fish, yellow tail kingfish and mackerel scad) and number of prey. Although our RMT model (Figure 2) shows that masked boobies consumed prey that differed in their macronutrient composition, supporting previous findings by Lenky et al. (2012) and Tait et al. (2014), both sexes had diets with

similar macronutrient (protein and lipid) and energy yield content. Our dietary analysis did not find undigested hard parts (e.g. otholiths or cephalopod beaks) that could influence this sex-specific comparison. However, it is likely that this result could be subject to the caveat of the small sample size. Therefore, dietary sexual differences related to sex-specific macronutrient foraging strategies for this species remains to be tested.

Bio-logger deployments in predators have previously been used to assess energy intake following the optimal foraging theory (OFT) of Stephens & Krebs (1986). Most vertebrate species, including carnivore predators, ingest a mixed diet suggesting that factors other than energy are fundamental to their needs (Hailey et al. 1998). The combination of miniaturised cameras with AB models showed that both birds captured similar prey (flying fish), but differed in the overall nutrient intake (Figure 3). This difference is likely related to the number of prey consumed and also to the differences in the macronutrient composition of prey that is influenced by their size, sex, age and breeding stage (Montevecchi & Piatt 1984; Tait et al. 2014). The differences in macronutrient composition of prey provide evidence that marine predators forage in complex nutritional marine environments. It remains to be established whether predators in the wild are likely to feed selectively from the prey available according to nutrient composition, in order to maximise fitness as previously observed in laboratory studies (reviewed in Simpson & Raubenheimer 2012).

Challenges and future directions

The results presented here are subject to the caveat that we were unable to obtain a larger sample size and this is likely to influence the macronutrient composition of the estimated diets and potential sex comparisons. In addition, our cameras weigh 70 g and are suitable for deployment only on relatively large species. Based on the benefits and limitations of the use of cameras (Moll et al. 2007), there are several trade-offs that remain to be considered for the future of this form of bio-logging. First, balancing the need for continuous filming for extended periods versus the addition of other on-board sensors (e.g. global positioning systems, time depth recorders, accelerometers, temperature loggers) to enhance the information collected. Second, optimising battery selection to meet the power demands of the bio-logger while adhering to the weight and size constraints imposed by the target animal. Studies in which researchers are not able to collect undigested prey samples simultaneously with videography from the miniaturised cameras can utilise this valuable high-resolution tool to garner an estimate size of prey consumed from morphological features within the field of view of the camera lens (e.g. beak length, maximum width of turtles' head; see more details in Machovsky-Capuska et al. 2011; Heaslip et al. 2012). Furthermore, representative prey samples matching the size of prey identified from the video footage should be collected for proximate composition analysis (Tait et al. 2014) and the data can be then modelled using NG following the present study.

Overall, our results provide insights into carnivore nutritional ecology and represent the first example that highlights the significance of combining bio-logging science with NG. This approach should be considered in future studies that aim to contribute to the general understanding of the behavioural and physiological mechanisms, and ecological and evolutionary significance of animal foraging (e.g. energy expenditure budgets and prey selection for self- and offspring feeding that could lead to sex-specific foraging

strategies). In particular, it can provide an invaluable contribution to our understanding of whether the foraging behaviour of a predator in the wild is related to their nutritional state and how this might influence the way they exploit their environment. Such information can be instrumental for enhancing conservation measures for endangered species (e.g. habitat conservation), monitoring the fate of rehabilitated animals post-release and managing human-wildlife conflict (e.g. fisheries interactions).

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