

# Breeding Stage and Environmental Factors Affect Prey Selection by Greater Crested Terns Off Southeast Australia

Katrin Quiring (✉ [katrin.quiring@students.mq.edu.au](mailto:katrin.quiring@students.mq.edu.au))

Macquarie University <https://orcid.org/0000-0002-3550-6031>

**Gemma Carroll**

University of Washington

**Eckhard Heymann**

Georg-August-Universität Göttingen

**Curtis Champion**

Southern Cross University

**Robert Harcourt**

Macquarie University

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# Abstract

Variation in the diet of marine predators such as seabirds can be used to track environmentally-driven changes in ocean ecosystems. However, studies of predator diet must account for intrinsic influences on prey selection, such as changing nutritional requirements during breeding. Using digital photography, we investigated how the type and size of prey brought back to the colony by greater crested terns (*Thalasseus bergii*) changed in relation to breeding stage, and to variation in oceanographic conditions around Montague Island, Australia (36°15'S, 150°13'E). 2469 prey items were identified to species or family level over 35 consecutive days of photo-sampling in 2018. Australian anchovy (*Engraulis australis*), a surface-schooling clupeid fish, was the most abundant prey returned to the colony during all breeding stages (84.5%). The proportion of anchovy increased from 77.0% when birds were provisioning their adult partners during incubation, to 92.4% when they were provisioning chicks, suggesting selective foraging behaviour on this energy-dense species as a means to facilitate rapid chick growth. Anchovy size was largest during incubation ( $91.1 \pm 14.9$  mm), smallest during early chick provisioning ( $71.8 \pm 11.0$  mm), and increased slightly during mid-provisioning ( $79.6 \pm 11.9$  mm), indicating adaptive prey selection that is matched to the physical requirements of different breeding stages. The proportion of anchovy prey was also influenced by extrinsic environmental factors, with anchovy becoming more dominant with increasing local sea surface temperatures, up to  $\sim 17.5^\circ\text{C}$ . Our findings highlight the importance of examining both intrinsic and extrinsic determinants of diet composition across breeding stages in seabird populations.

## Introduction

Upper trophic-level predators such as seabirds can act as sentinels of changes in marine ecosystems, with their demography, behaviour and physiology reflecting variability in oceanographic and ecological conditions (Hazen et al. 2019). For example, temporal changes in the occurrence, abundance and size of prey that seabirds consume can be used as indicators of food availability and ecosystem structure (Suryan et al. 2002; Parsons et al. 2008), and can provide an early warning of anthropogenic impacts on food webs (Green et al. 2015). Monitoring seabird diets can therefore be an important tool to inform conservation biology and ecosystem-based fisheries management (e.g. Lorentsen et al. 2018; Thayne et al. 2019; Hazen et al. 2019).

During the breeding season, the foraging range of seabirds is constrained by central-place foraging, which requires individuals to return to the colony between foraging trips to incubate eggs or provision their young (Cairns 1988). This means that birds must forage efficiently on available prey that is within a relatively short distance of the colony. Optimal foraging theory for central-place foraging predicts that *single-prey loaders* (species including guillemots and terns that carry a single whole prey item per foraging trip back to the colony) should maximise the energy load per unit foraging by providing larger, or energetically richer prey to their chick than they feed themselves (Orlans and Pearson 1979). For instance, adult crested terns (*Sterna bergii*) conduct short foraging trips close to the colony to provision their offspring several times a day with small single prey items (McLeay et al. 2010). This behaviour is

assumed to be adjusted to energetic requirements and ingestion capabilities of chicks. Therefore, during provisioning, single-prey loaders should bring back small fatty fish that are energy dense, selecting increasingly large fish as the chick grows (Batchelor and Ross 1984). This contrasts with the foraging strategy of *multiple-prey loaders* (e.g. auks carry multiple prey items per foraging trip in the bill; Procellariiformes regurgitate stomach oil), which do not have the same constraints on the selection of individual prey items, but should maximise the energy load per foraging trip, especially if they travel large distances from the breeding colony (Orlans and Pearson 1979).

While intrinsic constraints imposed by provisioning requirements may influence prey selection during breeding, the availability of prey also varies with extrinsic environmental conditions. Temporal variation in oceanographic variables can have a strong effect on the foraging success of seabirds, which can impact their body condition, growth and ultimately reproductive performance (Harwood et al. 2015). This is particularly true when birds undertake central place foraging during breeding, as they are restricted to finding prey within a limited distance from the colony and cannot move to more favourable foraging areas. For instance, a long-term study on king penguins suggests that anomalies in sea surface temperature (SST) adversely affected breeding success as birds had to dive deeper and farther from the colony to forage on favoured prey (Bost et al. 2015). Similarly, a shift in the diet of black guillemots (*Cepphus grylle*) from Arctic cod (*Arctogadus glacialis*) to demersal fish during a period of decreasing sea ice and increasing SST, led to slower chick growth, low fledgling mass and an increase in chick starvation (Divoky et al. 2015). In addition, prey availability may be altered at shorter time scales, such as in response to weather (White 2008). Prey capture under adverse weather conditions can be mediated by poor flight performance, or reductions in prey detectability or catchability (Elliott et al. 2014; Kogure et al. 2016). There is evidence that, for example, high wind speeds influence foraging success in seabirds, as indicated by a decrease in dominant prey, as well as a reduction in prey energetic value and size (Stienen et al. 2000; Howells et al. 2017). Accordingly, the interplay of both intrinsic (i.e. physical requirements of chicks vs. adults) and extrinsic (environmental variability) processes affecting diet composition should be accounted for when interpreting seabird diet data.

Some seabird species bring whole fish back to the colony in their bill to provision their chick or partner at the nest. In the past, experienced researchers have used binoculars to directly identify prey types, a technique that facilitates large samples being collected over short periods, and allows documentation of seasonal variation in prey choice (Rodway and Montevecchi 1996). While this sampling approach is feasible in low diversity ecosystems where birds bring back only a few types of prey, it is challenging in complex food webs where birds consume a broad suite of prey types or carry multiple prey items in their bill (Barrett et al. 2007). This method is limited by observer bias that can result in the misidentification of prey and can undermine taxonomic resolution, especially when there are no independent means by which to verify observations (Larson and Craig 2006). Recent advances in digital photography overcome many traditional observer-based limitations, with the potential to provide a verifiable, non-invasive tool to study seabird diets. Photographing birds with prey at the colony allows researchers to identify a large number of prey items with greater taxonomic precision and to estimate the size of prey being selected, while facilitating re-analysis and verification of species if necessary (Gaglio et al. 2017).

Greater crested terns (*Thalasseus bergii*) are small coastal seabirds with an extensive breeding range that encompasses the Australian coastline. Terns are nearshore foragers that mostly acquire food by dipping onto the sea surface or diving up to one metre below the surface (Crawford et al. 2005). During breeding, they are central place foragers with adult pairs taking turns to leave the colony to provision themselves and to bring prey back for their partner or offspring. During incubation, a single-prey item is brought to the partner for display or as a gift in courtship. Assuming that the prey brought back for the partner is equivalent to the prey consumed by birds at sea, this is an indication of the diet composition of the adult population. Once the chick hatches, both parents deliver single-prey items to their offspring. The bill-loading behaviour of terns makes it possible to quantify trends in prey type and size using a digital camera and a telephoto lens without disturbing the colony. Digital photography has previously been used to describe the diet of *T. bergii* in South Africa, doubling the known diversity of prey species compared to traditional regurgitate sampling, and providing accurate and precise measurements of prey length (Gaglio et al. 2017).

This study aims to identify intrinsic (i.e. physical requirements of chicks vs. adults) and extrinsic (environmental) determinants of diet composition of greater crested terns at a key southern-eastern Australian breeding site, Montague Island, during the 2018 breeding season. Specifically, we use digital photography as a non-invasive sampling technique to assess variation in diet composition (prey type and size) between breeding stages (incubation and chick provisioning), and to determine whether short-term variability in environmental covariates influences diet composition. First, we investigate the trade-off made by single-prey loaders between maximising energy intake per foraging trip, and ensuring that prey can be physically swallowed by the chick (Orians and Pearson 1979). We predict that (1) the proportion of anchovy in the diet will increase during provisioning stages, because this is an abundant, lipid-rich prey that can facilitate the rapid growth of small chicks (Batchelor and Ross 1984). Similarly, we predict that (2) anchovy standard length (SL) will decrease during early provisioning when chicks are small, then increase during mid-provisioning as parents adjust prey size in accord with the ingestion capabilities of growing chicks. Second, we analyse shifts in diet composition of greater crested terns in response to short-term variation in environmental variables. Specifically, we predict that (3) the proportion of anchovy will decrease under adverse environmental conditions such as strong winds, high SST or high waves, which are factors likely to influence the availability or catchability of surface-schooling prey.

## Methods

### Study site and species

This study was undertaken on Montague Island (36°15'S, 150°13'E), an 81 ha nature reserve located approximately 9 km off the coast of southeast New South Wales, Australia. Greater crested terns nest in the open on the island at high densities. The tern colony on Montague Island comprises multiple sub-colonies; this study was conducted on the largest and most accessible one, consisting of ca. 1000 breeding pairs in 2018 (Fig. 1a; counted from a wide-angle photograph of the colony taken on 20 October 2018). The study was conducted over 35 consecutive days from 2 October to 5 November during the

2018 greater crested tern breeding season. As chicks hatch synchronously across the colony, the first chick sighting was selected as the day of hatching and the start of provisioning (here: 23 October 2018 - study day 22). Breeding stages were classified as incubation, early provisioning and mid provisioning, and the study covered the full period from incubation to mid provisioning. During incubation, partners alternatively incubate the nest and bring single-prey items to their mate for courtship and pair-bonding. Early provisioning comprised the week following hatching during which both parents provision the chick in the nest cup, and mid provisioning the subsequent week when chicks start to move around the nest (Gaglio et al. 2018).

## Photographic sampling

Greater crested tern diet was investigated using digital photography to assess differences between adults and chicks in the size and type of prey consumed over the course of the study period. Adult terns carrying prey in their bill were photographed as they returned to the colony (Fig. 1a). Photographs were taken using a Canon (Tokyo, Japan) 50D camera fitted with a Canon EF 70-300mm f/4.0-5.6 IS USM tele zoom lens. Camera settings were mostly applied following Gaglio et al (2017), with the following settings: i) shutter speed priority 1/2500–1/4000 s depending on light conditions, ii) automatic ISO, iii) high-speed continuous shooting, iv) autofocus on AI servo (autofocus system for continuous tracking of moving subjects), and v) large Jpeg file format. The tele zoom lens was set to autofocus with the image stabiliser on.

Every day, photos of birds arriving with prey at the colony were taken continuously during three two-hour sessions (morning session from 0700–0900 hr, midday session from 1100–1300 hr and afternoon session from 1500–1700 hr AEST; after daylight savings from 0800–1000 hr, 1200–1400 hr and 1600–1800 hr AEDT). Photos were taken from a different vantage point during each session to account for sun position. Photos were taken as a photo-set consisting of three images, with the sharpest selected for prey identification and measurements. The distance between the vantage points and the closest bird was approximately 5 m. The birds did not show any sign of stress or disturbance due to the presence of the photographer.

## Identification of prey species

All blurred and unclear images (due to e.g. distance, position of prey in the bill, lighting etc.) were excluded from the analyses. From the remaining photographs, prey was identified to the highest possible taxonomic resolution, based on morphological characteristics (Fig. 1b-k). Fish identification was undertaken by comparing photographs with published images and fish identification guides from the Australian Museum (<https://australian.museum/learn/animals/fishes>), and subsequently verified by multiple species experts from the NSW Department of Primary Industries and the University of New South Wales, Australia.

## Estimation of anchovy size

Australian anchovy (*E. australis*) is a common species in the diet of crested terns in Australia (McLeay et al. 2009a). Therefore, this species was chosen as a standard by which to compare the size of prey brought back to the colony during different breeding stages. However, with prey tending to flex in the bill, direct measurements of standard length (SL; the length from the tip of the snout to the posterior end of the hypural plate) from images may underestimate true fish length (Gaglio et al. 2017). Nevertheless, accurate estimates of SL can be obtained by extrapolating from measurements of individual body parts such as eye diameter, head width and operculum width that are easier to measure from photographs. Accordingly, for each image, the 'line selection tool' in the image analysis software IMAGEJ (Schneider et al. 2012) was used to estimate eye diameter, head and operculum width of each fish by scaling the pixel length in the image to the mean culmen length of crested terns (61.2 mm; Crawford et al. 2005). Using log linear allometric regressions, three estimates of SL were obtained (see Table S1 in Gaglio et al. 2017):

1. Eye diameter (E):  $SL = -68.16 + 91.95 \times \ln(E)$
2. Head width (H):  $SL = -168.70 + 112.29 \times \ln(H)$
3. Operculum width (O):  $SL = -230.44 + 121.60 \times \ln(O)$

The arithmetic mean of these three measurements was used in further analyses including anchovy SL. An example of the application in IMAGEJ is provided in Fig. 2 and detailed information on the accuracy and precision of the methodology is given in Gaglio et al (2017).

Importantly, Gaglio et al (2017) used the European anchovy (*E. encrasicolus*) to create regressions for anchovy eye diameter, head and operculum width, and these equations were applied to measurements of Australian anchovy in this study. The morphometric characteristics of both species are very similar, although the European anchovy is slightly larger than the Australian anchovy (average length: 13.5 cm vs. 12 cm; Whitehead et al. 1988). Since this study aims to compare relative fish length within the sample rather than illustrating variability in absolute fish length, regression equations calculated for European anchovy were used with the caveat that these measurements may consistently bias the true length of Australian anchovy photographed in this study.

## Environmental factors

Key environmental variables that are likely to influence either the distribution or abundance of prey species in the greater crested terns' foraging range, and/or the terns' ability to catch them were selected for analysis. These included wind speed, sea surface temperature (SST) and wave height. Wind speed (km/h) was recorded by the Australian Bureau of Meteorology weather station located at the lighthouse on Montague Island ([www.bom.gov.au](http://www.bom.gov.au)). Wind measurements were made using an automatic anemometer with an accuracy of +/- 5% of the wind speed for wind speeds greater than or equal to 10 m/s. Wind data were downloaded at a 30 min resolution, each measurement representing the average of the 10 min period prior to the observation time.

Gap-free daily records of satellite-derived SST at a 0.05° x 0.05° spatial resolution were measured by the UK Met Office's Operational Sea Surface Temperature and Ice Analysis (OSTIA) system (downloaded from

marine.copernicus.eu). Based on previous observations of the tern's foraging range from Montague Island (O'Hara 2016), SST values were averaged across an area spanning 35° to 37° north to south, from the coast out to the edge of the continental shelf (i.e. 200 m depth isobath). Because SST was available at a daily temporal resolution, daily values were assigned to multiple photography sessions within a day.

Wave height (m) was recorded by the NSW Department of Planning, Industry and Environment's (DPIE) Batemans Bay offshore Waverider buoy (35°44'25", 150°19'03"; <https://mhl.nsw.gov.au/Station-BATBOW>; approximately 53 km north of Montague Island). Data were recorded in bursts (lasting approximately 34 minutes long starting on the hour) at 0.5-second intervals. Wave height for each of these periods is defined as the mean height of the largest 33% of waves.

Previous GPS tracking work on Montague Island showed that tern foraging trips last an average of two hours (O'Hara 2016). Hence any photo taken at the colony during a two-hour sampling period could reflect foraging conditions up to two plus hours earlier than the actual sampling time. Therefore, wind and wave data were assigned to a photo session by taking an average of each variable across a four-hour period starting two hours prior to each session.

## Data analysis and statistics

The number of each prey species as a proportion of the total number of prey photographed throughout the study period was calculated to quantify the diet composition of greater crested terns during the 2018 breeding season on Montague Island. Key prey species, i.e. species making up > 1% of the diet, were identified to simplify graphical illustrations and statistical analyses. The proportion of each prey type was calculated for each two-hour photo session, and linked to information on breeding stage (incubation, early provisioning, mid provisioning) to compare prey brought back for adults (during incubation), and for chicks (during provisioning stages).

A chi-squared goodness-of-fit test was conducted to assess differences in diet composition between incubation and chick rearing. A generalised linear mixed model (GLMM) with beta error structure and logit function was used to investigate the effect of breeding stage on the proportion of anchovy returned to the breeding colony by adult terns. Prior to analysis, the response variable (anchovy proportion) was compressed to avoid absolute values of zero or one by taking  $y = (y^*(n-1) + 0.5)/n$ , where  $n$  is the sample size (Smithson and Verkuilen 2006). The model was fitted in R using the package 'glmmTMB' (version 1.0.1; Brooks et al. 2017). Similarly, a linear mixed model (LMM; R package 'lme4'; Bates et al. 2015) was used to investigate the effect of breeding stage on the dependent variable anchovy SL. Each of the models included breeding stage (three levels: incubation, early provisioning, mid provisioning) as fixed term and study day ( $N = 35$  days) as crossed random effect to account for the repeated three-session per day design. Finally, a post-hoc test was performed using the package 'emmeans' (version 1.4.6; Lenth 2020) to investigate the effect within each breeding stage category. Results were Tukey-adjusted for multiple testing. For all analyses, model assumptions were checked following Zuur et al (2009).

To visualise differences in prey composition in relation to breeding stage, a non-metric multidimensional scaling plot (NMDS) was generated using the R package 'vegan' (Oksanen 2011). NMDS is an ordination technique to represent the position of data points in multidimensional space using distance measures and a reduced number of dimensions (typically 2). The Bray-Curtis dissimilarity index was used to create a distance matrix that reflects the multidimensional distance between data points with objects grouped closer together being more similar. Ellipses were plotted to depict the centroid and inertia of each breeding stage.

Generalised additive mixed models (GAMMs) using a beta regression and logit function were used to assess the influence of environmental variables (SST, wave height, wind speed) on the proportion of prey species in the diet. GAMMs, as an extension to GLMMs, allow an estimation of potential non-linear relationships between continuous explanatory variables and the response. The models were fitted using the R package 'mgcv' (version 1.8–31; Wood 2006). Smoother terms were applied to explanatory environmental variables and were generated using regression splines. Explanatory variables also included breeding stage as a fixed effect and study day as crossed random effect to account for intraclass correlations among day-specific sampling events. An alpha level of 0.05 was used to determine statistical significance. All statistical analyses were carried out in R (v3.5.3; R Development Core Team 2017).

## Results

### Diet composition

Over the 35 consecutive days of photo sampling, 3280 photo-sets were taken, yielding images of 2469 prey items identifiable to species or family level. 1265 prey items were identified during incubation and 1204 items during provisioning (early provisioning:  $n = 482$ , mid provisioning:  $n = 722$  prey items). Single prey items brought back to the colony were almost exclusively fish, with only one cephalopod species identified during the 2018 breeding season (Table 1).

Seven main prey types were identified of which Australian anchovy (84.5%) was the dominant species followed by barracouta (*Thyrsites atun*; 4.9%), trevally spp. (Centrolophidae spp.; 3.5%), goatfish spp. (Mullidae spp.; 1.9%), bluebottle fish (*Nomeus gronovii*; 1.4%), southern calamari squid (*Sepioteuthis australis*; 1.1%) and eastern sea garfish (*Hyporhamphus australis*; 1.1%; Table 1). Remaining prey items making up a total abundance of  $< 1\%$  over the breeding season were summarised as 'other fish' to simplify graphical illustration.

Table 1

Numbers and proportions of prey species photographed in the bills of greater crested terns returning to the colony on Montague Island in 2018 according to the breeding stage of the terns. A total of 2469 prey items were identifiable to species or family level of which 1265 prey were identified during incubation (adult diet) and 1204 during provisioning stages (chick diet).

Common name	Scientific name	Family	adult N	%	chick N	%	total N	%
Australian anchovy	<i>Engraulis australis</i>	Engraulidae	974	77.0	1112	92.4	2086	84.5
Barracouta	<i>Thyrsites atun</i>	Gempylidae	114	9.0	6	0.5	120	4.9
Trevally spp.	Indet. spp.	Centralophidae	76	6.0	10	0.8	86	3.5
Goatfish spp.	Indet. spp.	Mullidae	7	0.6	40	3.3	47	1.9
Bluebottle fish	<i>Nomeus gronovii</i>	Nomeidae	12	0.9	22	1.8	34	1.4
Eastern sea garfish	<i>Hyporhamphus australis</i>	Hemiramphidae	20	1.6	7	0.6	27	1.1
Southern calamari squid	<i>Sepioteuthis australis</i>	Loliginidae	27	2.1	1	0.1	28	1.1
Redbait	<i>Emmelichthys nitidus</i>	Emmelichthyidae	22	1.7	0	0.0	22	0.9
King gar	<i>Scomberesox saurus</i>	Scomberesocidae	7	0.6	1	0.1	8	0.3
Silver sweep	<i>Scorpius lineolata</i>	Scorpididae	5	0.4	2	0.2	8	0.3
Pilotfish	<i>Naucrates ductor</i>	Carangidae	1	0.1	1	0.1	2	0.1
Flying fish spp.	Indet. spp.	Exocoetidae	0	0.0	1	0.1	1	0.04

Anchovy was the most common prey during all breeding stages but the diet was more diverse during incubation compared to early provisioning (Fig. 3–4). During incubation, in addition to anchovy, other prey such as barracouta, trevallies and southern calamari squid were frequently brought back to the colony but their abundance decreased once chicks hatched. In contrast, species such as bluebottle fish and goatfish occurred more frequently in the diet of crested terns provisioning chicks, compared to incubation (Table 1).

There was a significant difference in the proportion of anchovy between incubation (adult diet) and chick provisioning (Chi-square test,  $X = 13.72$ ,  $P < 0.01$ ), with terns showing a lower preference for anchovy when bringing prey back to the adult partner for courtship or display. Specifically, the mean proportion of anchovy in the diet increased significantly from 77.0% to 92.9 % once chicks hatched (early provisioning). During mid provisioning the proportion of anchovy was 91.9%. This was significantly higher than during incubation, but not significantly different from early provisioning (Fig. 5a). Statistical results for differences in anchovy proportions between breeding stages are summarised in Table 2.

Table 2

Effect of breeding stage (incubation, early provisioning, mid provisioning) on the proportion of anchovy in the diet of greater crested terns in 2018. Mean (%) anchovy proportion and Tukey test adjusted p-values from comparisons across breeding stages are presented.

Dependent variable	Breeding stage	Mean (%)	Estimate	Std. Error	z-ratio	p-value	
						Early prov.	Mid prov.
Anchovy proportion	Incubation	77.0	-0.957	0.277	-3.459	< 0.01	0.046
	Early prov.	92.9	-0.648	0.268	-2.414		0.62
	Mid prov.	91.9	0.309	0.332	0.931		

## Anchovy size

Based on measurements from 423 suitable images, the standard length (SL) of anchovies brought back to the colony ranged from 19.7 mm to 143.4 mm. Anchovies were largest during incubation when birds were bringing fish back for their partner (mean  $\pm$  SD =  $91.1 \pm 14.9$  mm,  $n = 193$ ). There was a significant decrease in anchovy SL to a mean size of  $71.8 \pm 11.0$  mm,  $n = 84$  during early provisioning (Fig. 5b), suggesting a preference for smaller sized fish when provisioning small chicks. Anchovy SL increased slightly to  $79.6 \pm 11.9$  mm,  $n = 146$  during mid provisioning which was significantly smaller than incubation, but not significantly different from the early provisioning stage (Table 3).

Table 3

Effect of breeding stage on anchovy standard length (mm) estimated from photo-samples ( $n = 423$ ) of greater crested terns in 2018. Mean (SD) and Tukey test adjusted p-values from comparisons across three breeding stages, incubation ( $n = 193$ ), early provisioning ( $n = 84$ ), and mid provisioning ( $n = 146$ ) are presented.

Dependent variable	Breeding stage	Mean (SD) mm	Estimate	Std. Error	z-ratio	p-value	
						Early prov.	Mid prov.
Anchovy SL	Incubation	91.1 (14.9)	18.24	5.18	3.52	< 0.01	0.05
	Early prov.	71.8 (11.0)	12.07	4.93	2.45	–	0.58
	Mid prov.	79.6 (11.9)	-6.17	6.15	-1.00	–	–

# Diet composition in relation to environmental factors

The GAMM revealed that the proportion of anchovy in the diet of greater crested terns increased with warmer SSTs, with the rate of increase slowing slightly at SSTs above 17.5°C (Fig. 6a). None of the environmental variables wind speed or wave height had a significant influence on the proportion of anchovy returned to the breeding colony (Table 4).

Table 4

Effect of environmental variables (SST, wave height, wind speed) on the proportion of anchovy in the diet of greater crested terns using generalised additive mixed models (GAMMs). GAMM results include breeding stage as fixed effect. Shown are the estimated degrees of freedom (edf), chi square and p-values for each environmental parameter, as well as the percent deviance explained as measure of model performance.

Dependent variable	Environmental variable (smooth term)	edf	Chi-square	p-value	Deviance explained
Anchovy proportion	SST	1.54	10.57	<b>0.02</b>	33 %
	Wave height	1.75	1.68	0.41	36.2 %
	Wind speed	2.22	3.67	0.22	44.7 %

## Discussion

Variation in the diet of marine predators can give important insights into variability in marine ecosystems (Hazen et al. 2019). However, when making inferences from predator diets, it is important to disentangle intrinsic drivers such as provisioning requirements on prey selection from extrinsic drivers such as environmental influences on prey availability. This study quantified the type and size of prey exploited by a marine predator, the greater crested tern, during the 2018 breeding season on Montague Island, Australia using photography of prey items brought back to the colony. In order to understand the interplay of intrinsic and extrinsic processes determining diet composition of this colonial seabird, prey selection relating to constraints imposed by breeding stage were investigated alongside the effects of daily variability in environmental conditions.

## Prey composition and size

Consistent with findings on diet composition of crested terns from diverse geographic locations and oceanographic systems, small surface-schooling clupeids, in this case anchovies, were the most abundant prey returned to the colony during the breeding season (Walter et al. 1987; Chiardia et al. 2002; McLeay et al. 2009a; Gaglio et al. 2018). Despite the dominance of anchovy in the diet during this study, greater crested terns still varied the type of prey caught at different stages of the breeding season. This flexibility and the differences in diet composition between adults and chicks are likely to reflect the need for terns to select appropriately sized prey to feed chicks during provisioning, as well as variation in the

availability of different prey types within the terns' foraging range at distinct times during the study period.

Barracouta - the second most abundant prey in the diet in our study – is also an important prey species of crested terns in South Australia (McLeay et al 2009a). Barracouta form large schools that feed on krill, squids and small fishes such as anchovy (Bray and Schultz 2020). Barracouta in southern NSW spawn in late winter (July-August) which may explain the occurrence of smaller (juvenile) barracouta in the diet of adult crested terns at the onset of the spring breeding season, but they may be too large for small chicks to swallow later in the season. Some demersal fish species, like bluebottle fish, are pelagic as juveniles, occurring near the sea surface where they are captured by crested terns at this life stage (Bray 2020). The southern calamari squid, in contrast, is a demersal species found in shallow inshore waters from the surface to 10 m depth (Norman 2000), making them available to seabirds foraging near the shore.

The proportion and size of anchovy returned to the breeding colony varied between incubation and chick provisioning, with chicks consuming a significantly higher proportion of anchovy than adults during early and mid provisioning. The high nutritional quality of clupeids like anchovy (Batchelor and Ross 1984, Pichegru et al. 2007) has been suggested to explain ontogenetic differences in diet composition between adults and chicks in greater crested terns in South Australia and the Benguela system in southwest Africa (McLeay et al. 2009b; Gaglio et al. 2018). Similar trophic segregation between adult and chick diets is found in other seabird species including great skuas (*Stercorarius skua*), sooty terns (*Onychoprion fuscatus*) and cape petrels (*Daption capense*) (Cherel et al. 2008; Fijn et al. 2012; Votier et al. 2003). We assume therefore that crested terns in this study selectively foraged higher trophic level (high quality) prey to provide their offspring in order to facilitate chick growth, which was different from the prey selected for an adult partner during incubation.

The differences in prey selection in this study highlight the ability of seabirds to make flexible foraging decisions based on prey quality, in order to maximise the growth and survival of their offspring. Previous work has shown that diet composition had a significant effect on chick growth and survival in kittiwakes with higher proportions of lipid-rich sandeel positively affecting daily growth rates in chicks (Christensen-Dalsgaard et al. 2018). Furthermore, an experimental study showed that feeding nestlings a lipid-poor diet impaired chick mass and cognitive abilities which likely accounted for an increase in mortality and low recruitment (Kitaysky et al. 2006). Similarly, the “junk-food hypothesis” has been proposed as the cause of breeding failure in a colony of common guillemots (*Uria aalge*) in the North Sea, following a switch in chick diets from high quality sandeel to sprat which is of significantly lower energy density (Wanless et al. 2005). In order to determine whether anchovy served as high-quality food facilitating offspring growth and survival in terns on Montague Island, future research should investigate chick body condition in relation to the proportion of anchovy returned to the colony each day. Although poorly studied and applied, methods of quantifying body condition non-invasively have been tested in free-living birds, for instance using thermal cameras to remotely link body temperature to physiological state (Jerem et al. 2018).

Anchovies were smallest during chick rearing. Due to their relatively small gullet, hatchlings are limited in the size of prey they can swallow and this means parents need to select prey according to the chick's capability. As chicks grow, parents may need to adjust to the increasing energetic requirements. As predicted by central-place foraging theory for single-prey loaders, adults may either increase the delivery rate or provide larger prey to growing chicks. The observed increase in anchovy size with chick age supports previous findings that there is size-selective predation by adult terns through the breeding season in response to changing energetic demands of nestlings (Hulsman et al. 1989; Shealer 1998; McLeay et al. 2009a; Gaglio et al. 2018). However, while these findings suggest active prey selection by adult terns in response to breeding stage, the influence of spatio-temporal availability of prey on diet composition should not be discounted.

## Environmental factors

Environmental characteristics, such as SST, drive the distribution and abundance of schooling fish, and thus the availability of prey to upper trophic levels in the ocean (Bertrand et al. 2008). In this study, SST was positively correlated with the proportion of anchovy returned to the breeding colony. In an earlier study at the same site, Carroll et al (2016) concluded that reduced prey capture of forage fish by little penguins (*Eudyptula minor*) associated with very low SSTs might reflect a period early in the season when water temperature had not been warm enough to facilitate phytoplankton growth, resulting in a lower local abundance of planktivorous fish. Likewise, SST > 21°C impaired prey capture success at the end of the penguin's breeding season, related to a stronger influence of the warm East Australian Current at this time (Phillips et al. 2020). Montague Island penguins have been shown to match the distribution of schooling forage fish like anchovy around the island when foraging, indicating that their prey capture success reflects local changes in prey availability that might be important for other sympatric predators such as greater crested terns (Carroll et al. 2017). Range-restricted species, such as breeding seabirds, may thus be particularly sensitive to the local availability of key prey species at crucial times in the breeding cycle (Crawford et al. 2006).

Breeding phenology in birds is likely timed to coincide with periods of peak resource availability. The prevalence of anchovy in the diet increased with SST in this study, and SST was seasonally elevated during chick provisioning stages (see online resources Fig. 1). It is possible that the timing of breeding is linked to elevated levels of production, indicated by greater proportions of energy-rich prey (e.g. anchovy) in the diet during chick provisioning. In support of the latter, anchovy abundance and availability to Peruvian seabirds increased during the period of chick provisioning with a peak around the time of fledging, suggesting breeding timing to be adjusted to optimal environmental conditions facilitating chick or fledgling survival (Passuni et al. 2016). Importantly, the extent to which a dietary shift in this study can truly be linked to prey availability and its influence by environmental covariates such as SST would require additional research on estimates of fish stock composition and abundance around Montague Island by, for example, local fishery assessments or acoustic surveys (e.g. Green et al. 2015; Carroll et al. 2017; Thayne et al. 2019).

# Conclusion

This study shows variability in the type and size of prey exploited by greater crested terns during the breeding season, indicating selective foraging behavior towards relatively energy-rich and smaller sized prey during chick provisioning. SST was positively correlated with the proportion of anchovy prey items, suggesting a link between extrinsic factors and prey availability in this marine ecosystem. While intrinsic processes require selective foraging behaviour regarding the type and size of prey required to meet the changing energetic demands of chicks, environmental conditions inherently dictate the availability of prey in the ocean. This supports the notion that breeding phenology in crested terns is timed to coincide with peak abundances of key prey and highlights the importance of examining both intrinsic and extrinsic determinants of diet composition and variability in seabird populations. The ultimate goal should be to simultaneously examine seabird diet composition and breeding parameters (e.g. chick body condition and survival) in response to oceanographic indices, as well as the spatial and temporal availability of prey in the ocean (Hazen et al. 2019). Compiling this knowledge is important for sustainably managing fisheries and to predicting anthropogenic impacts on marine populations in the future.

## Declarations

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### Authors' contributions

RH, GC, KQ conceived the ideas and designed the study; KQ collected the data; KQ and CC processed photographs and collated data; KQ and GC analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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### Data availability

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

### Compliance with ethical standards

## Conflicts of interest

The authors declare that they do not have conflicts of interest or competing interests.

## Ethics approval

This project was conducted under NSW NPWS Scientific Licence SL170064 at Macquarie University Animal Research Authority 2014-057. All applicable international, national, and institutional guidelines for the care and use of animals were followed.

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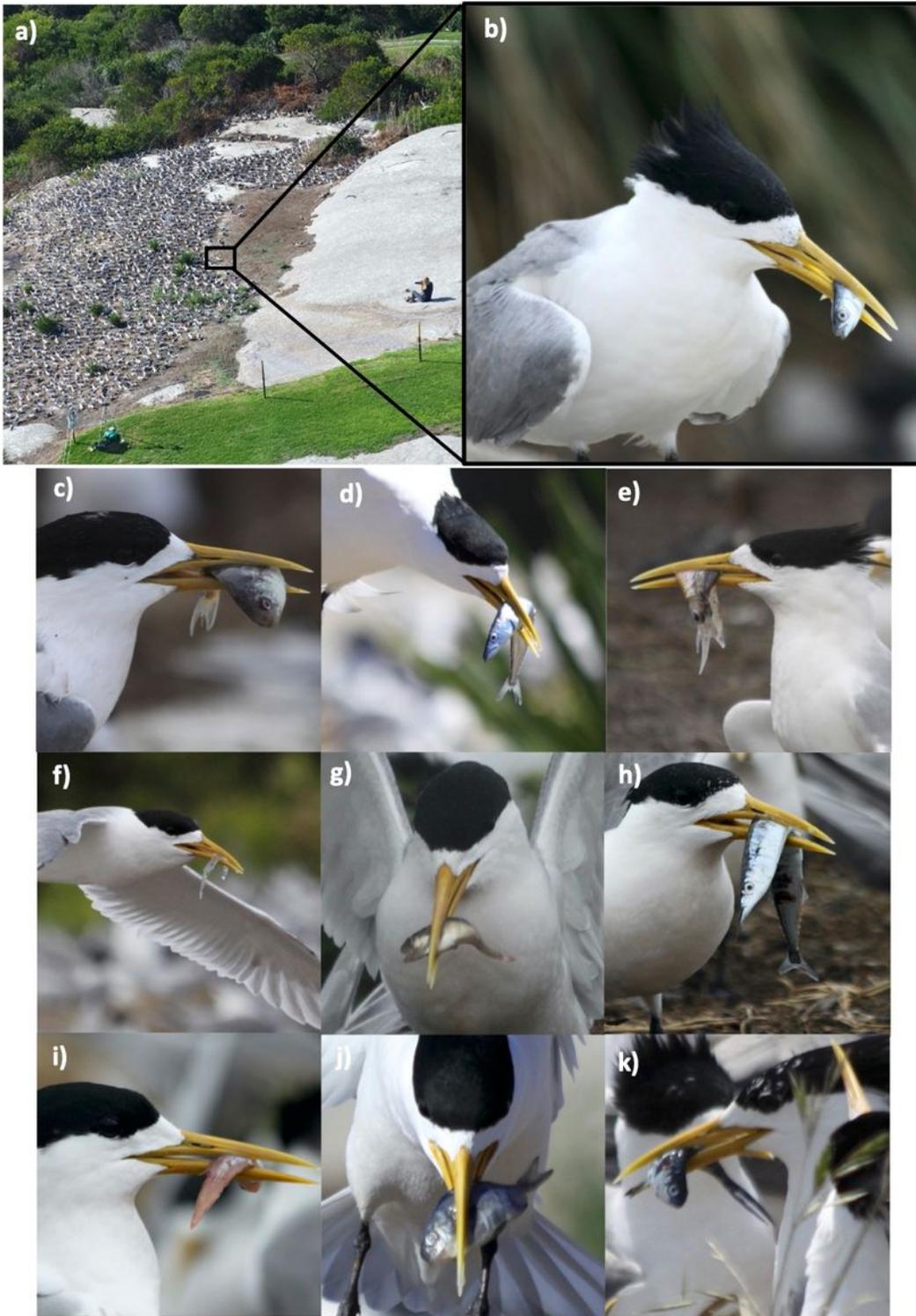
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## Figures



**Figure 1**

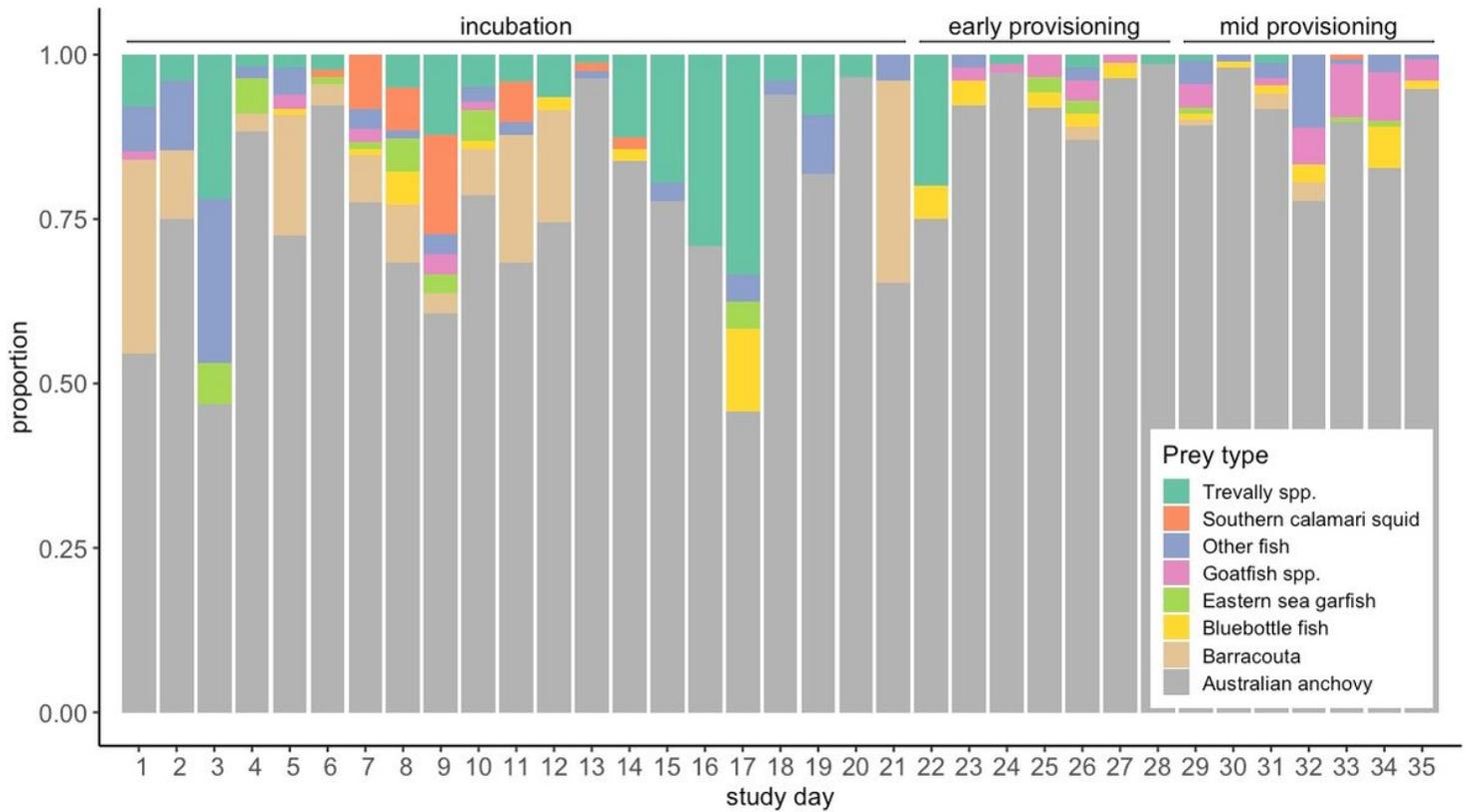
a) Photo of the greater crested tern colony taken from a lighthouse on Montague Island showing the photographer at vantage point 1 capturing photo-sets of adult terns carrying single-prey items to the colony at a distance that does not cause disturbance to nesting birds. b) The resulting close-up image of the prey used for identification and measurements. From b) to k) Examples of tern prey items: b) Australian anchovy, *Engraulis australis*; c) Trevally spp. (juvenile), *Centrolophidae* spp.; d) Barracouta,

Thyrsites atun; e) Southern calamari squid, *Sepioteuthis australis*; f) Eastern sea garfish, *Hyporhamphus australis*; g) Redbait, *Emmelichthys nitidus*; h) King gar, *Scomberesox saurus*; i) Goatfish spp. (juvenile), *Mullidae* spp.; j) Silver sweep, *Scorpius lineolata*; k) Bluebottle fish, *Nomeus gronovii*. Photo credit: Katrin Quiring, Lachlan Phillips



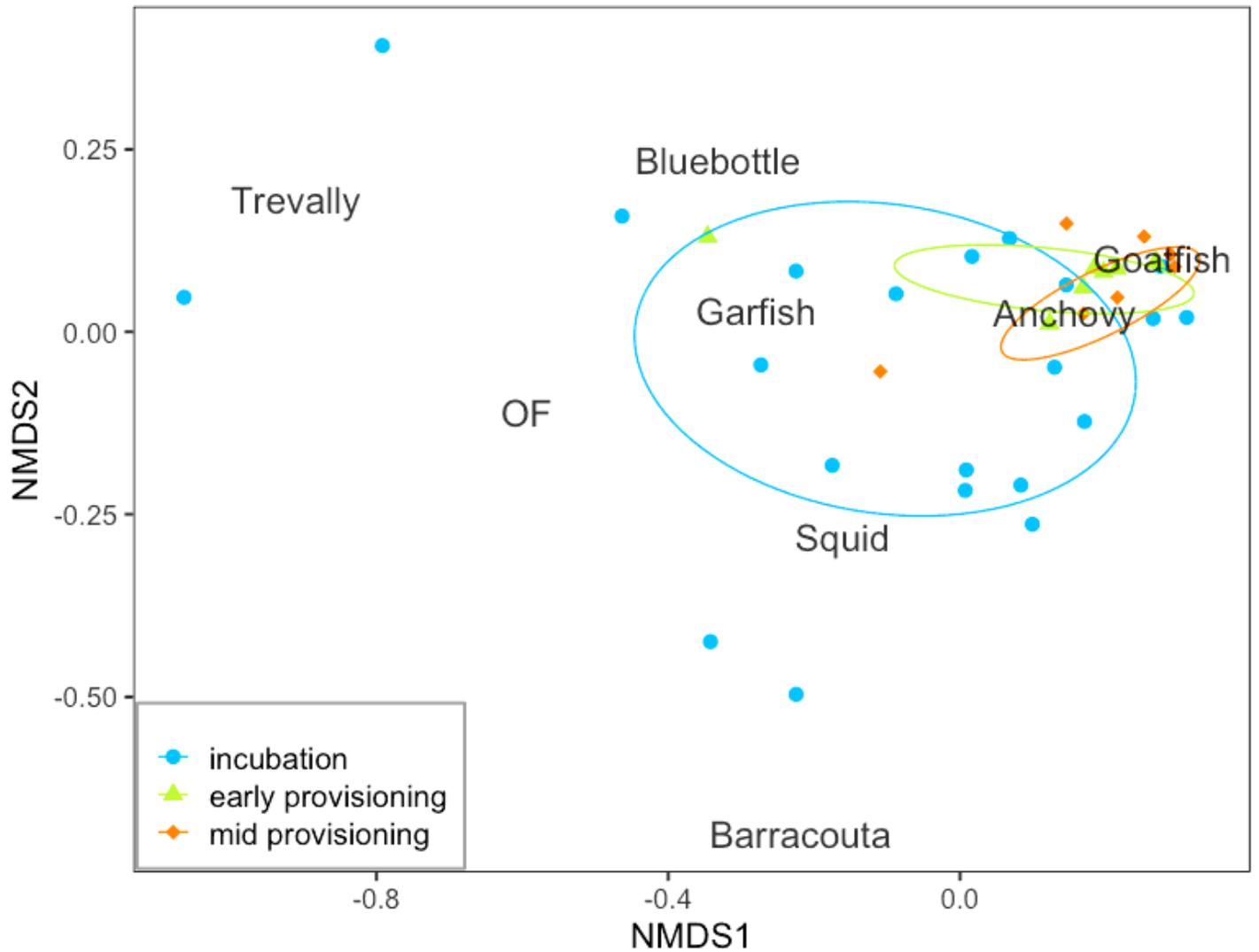
**Figure 2**

Example of the application (in IMAGEJ) of the 'line selection tool' to measure the linear distances for the three morphometric parameters: (1) eye diameter, (2) head width and (3) operculum width. Measurements were adjusted by scaling pixel length to the mean culmen length of greater crested terns. Method adapted from Gaglio et al (2017)



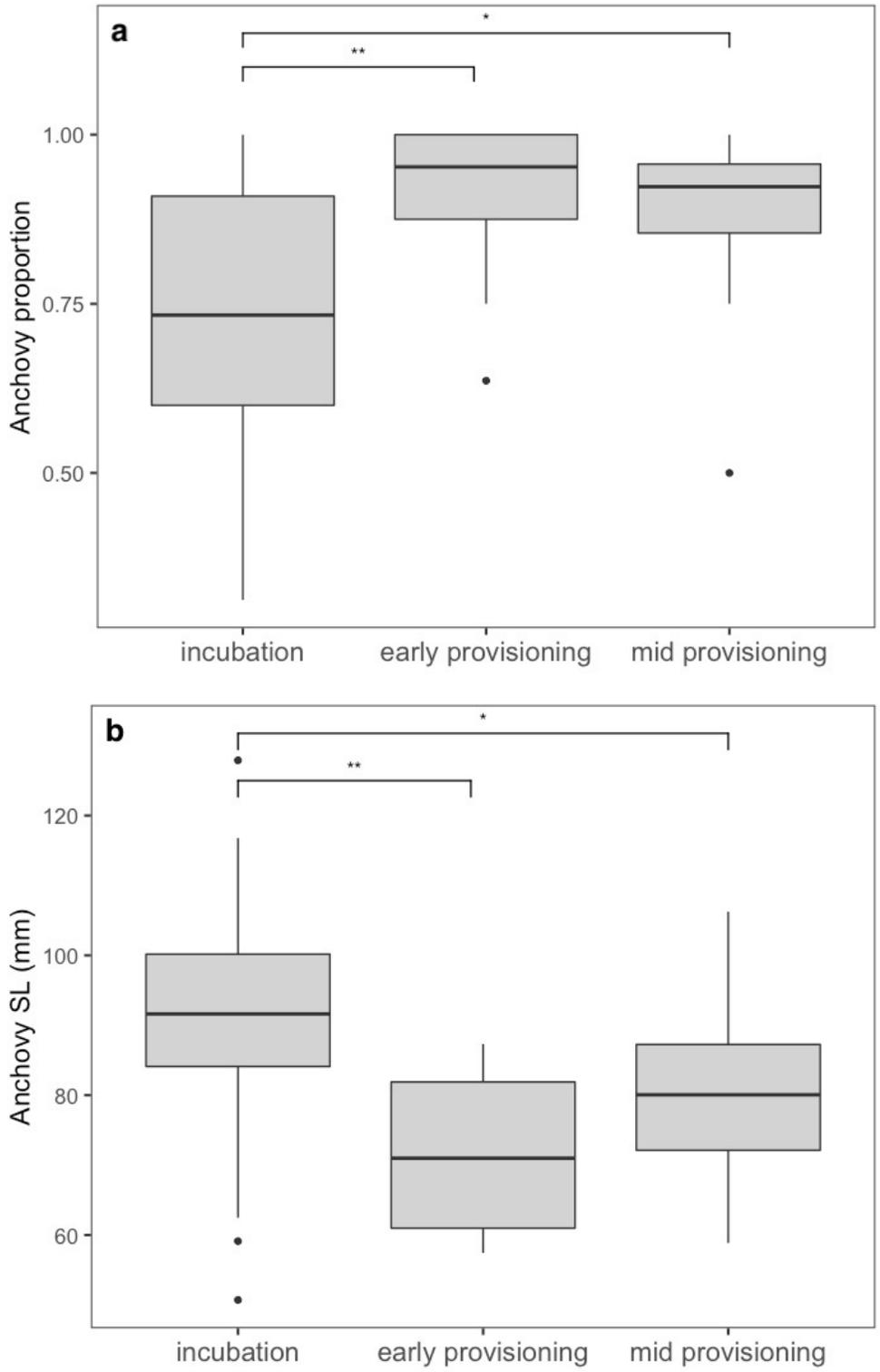
**Figure 3**

Daily variation in greater crested tern diet across study period (n= 35 days) and breeding stages: incubation (study day 1-21), early provisioning (study day 22-28), mid provisioning (study day 29-35). Depicted are the seven main prey species (Australian anchovy, barracouta, bluebottle fish, eastern sea garfish, goatfish spp., southern calamari squid, trevally spp.) and other fish returned to the breeding colony



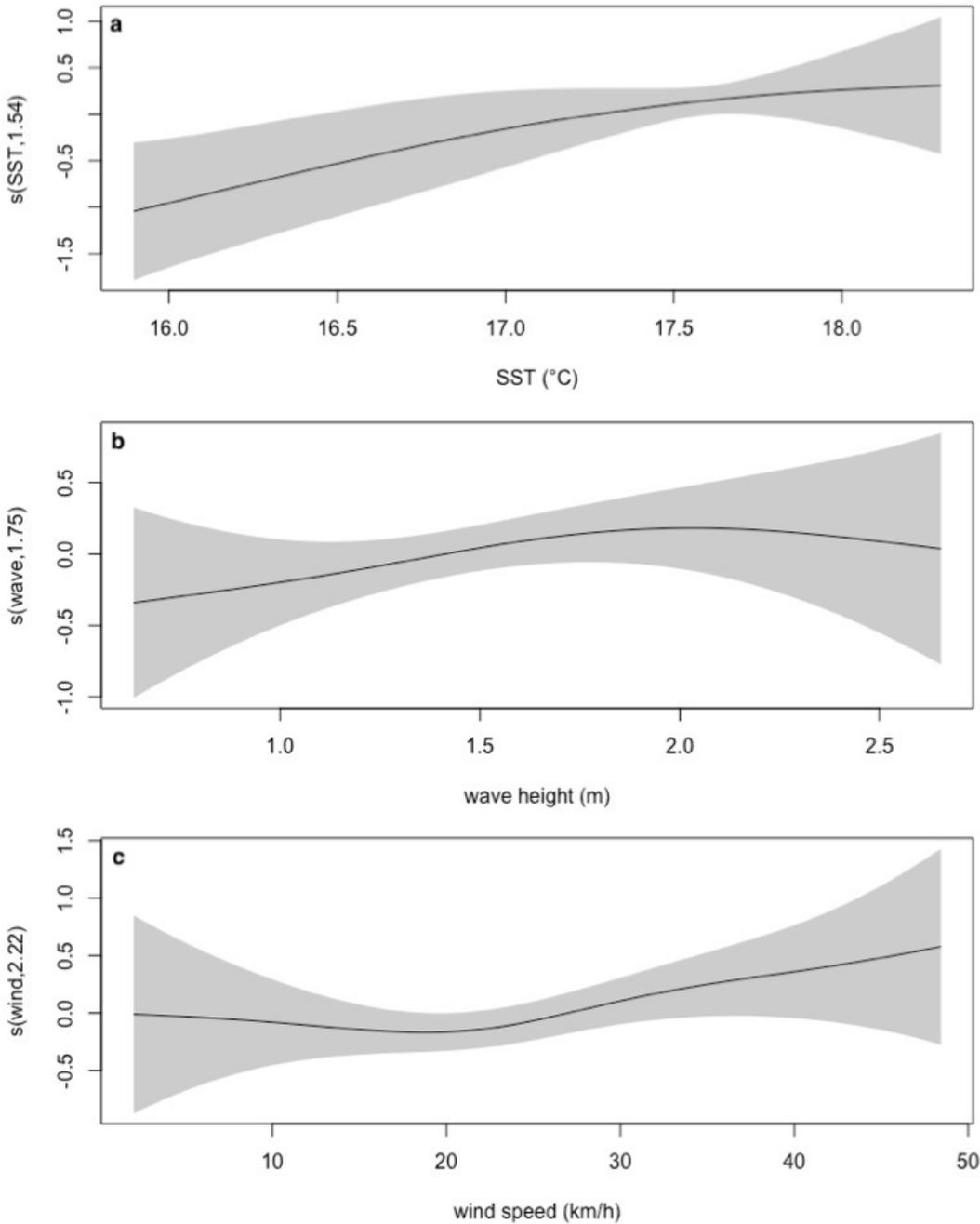
**Figure 4**

Non-metric multidimensional scaling plot (NMDS) of daily mean diet proportions showing differences in prey composition across three breeding stages (incubation, early provisioning, mid provisioning) by greater crested terns on Montague Island. Sample points represent each study day marked in different colours depending on breeding stage (see legend). Position of points is related to the relative daily contribution of each of the seven main prey species (Australian anchovy, barracouta, bluebottle fish, eastern sea garfish, goatfish spp., southern calamari squid, trevally spp.) and other fish (OF) returned to the breeding colony. Ellipses highlight the centre of gravity and inertia of each breeding stage



**Figure 5**

(a) The proportion of anchovy and (b) anchovy standard length (mm) in the diet of greater crested terns across three breeding stages (incubation, early provisioning, mid provisioning) on Montague Island in the 2018 breeding season. Box plots show the median and first and third quartile; whiskers extend to the 1.5 times the interquartile range. Black dots represent outliers. Significance levels are depicted as \* for  $p \leq 0.05$  and \*\* for  $p < 0.01$



**Figure 6**

Partial effects of environmental covariates (SST, wave height and wind speed) on the proportion of anchovy returned to the breeding colony in 2018.  $s(x,y)$  is the smoothing term, with  $x$  the explanatory variable and  $y$  the estimated degrees of freedom of the smoothing term. Pointwise 95% confidence intervals are shown for each model fit

## Supplementary Files

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