# **ORIGINAL PAPER**



# Assessing meal size in seabirds through head movement dynamics

Monserrat Del Caño¹ ○ · Flavio Quintana¹ ○ · Rory P. Wilson² ○ · Giacomo Dell'Omo³ ○ · Agustina Gómez-Laich⁴ ○

Received: 15 November 2024 / Accepted: 7 May 2025 © The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2025

#### **Abstract**

Parental food provisioning is crucial in avian breeding ecology, with significant implications for parental cooperation, sibling competition, and chick survival. Traditional methods for assessing food provisioning in marine birds involve direct observation, video recording, or more invasive techniques like chick weighing and regurgitation induction, which can be stressful for the birds and time-consuming. This study evaluates accelerometers as a less invasive alternative to quantify food provisioning behaviour in Imperial shags (*Leucocarbo atriceps*). Fieldwork was conducted at Punta León colony (43°04'S,64°29'W), Chubut, Argentina, between mid-November and mid-December of 2019, 2021, and 2022. Adult female shags were equipped with head-mounted accelerometers to monitor the intensity and duration of head movements during food delivery to their chicks. Data from 34 nests were collected, focusing on the relationship between chick age and food provisioning intensity within the first feeding session, which began when the female arrived at the nest with food and started feeding a chick, and ended when no chicks had been fed for 15 min. Our results suggest that head movement intensity (VeDBAsm) significantly influences meal size. Older chicks receive more food when adults exhibit more vigorous movements, while younger chicks do not receive additional food as movement intensity increases. This study demonstrates that accelerometry is a reliable and less invasive method for estimating the quantity of food transferred from parents to chicks older than 7 days. This approach enhances our ability to study Phalacrocoracidae provisioning behaviour while reducing disturbance, offering a valuable tool for future ecological and behavioural research in marine birds.

**Keywords** Accelerometry · Imperial Shag · Body mass · Meal size · Food provisioning

#### Responsible Editor: T. Clay.

☐ Monserrat Del Caño mdelcano@cenpat-conicet.gob.ar

Published online: 27 May 2025

- Instituto de Biología de Organismos Marinos (IBIOMAR), CONICET, Boulevard Brown 2915, U9120 ACD, Puerto Madryn, Chubut, Argentina
- <sup>2</sup> Swansea Lab for Animal Movement, Biosciences, College of Science, Swansea University, Singleton Park, Swansea SA2 8PP, UK
- <sup>3</sup> Ornis Italica, Piazza Crati 15, Rome 00199, Italy
- Departamento de Ecología, Genética y Evolución and Instituto de Ecología, Genética y Evolución de Buenos Aires (IEGEBA), CONICET, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria,

Ciudad Autónoma de Buenos Aires C1428EGA, Argentina

# Introduction

In birds, the study of parental food provisioning and chick begging behaviour is essential for understanding key aspects of breeding ecology (Trivers 1974; Price and Ydenberg 1995). A detailed quantification of these behaviours is important to determine which factors influence the distribution of food within a brood (Kacelnik et al. 1995), to analyse whether the degree of parental cooperation differs between sexes (Thaxter et al. 2009), and to determine if sibling hierarchy influences access to food (Safriel 1981; Forbes and Glassey 2000), among others. Such studies often require the collection of data on the frequency, timing, and amount of food each chick receives (Granadeiro et al. 1999; Gangloff and Wilson 2004; Low et al. 2012).

The ability to accurately estimate food provisioning varies among species, depending on their feeding strategies. In small passerines, direct observation is often sufficient, as adults carry visible prey in their beaks, allowing for identification and size estimation (Schwagmeyer and Mock 2008).



Similarly, in most raptors, adults deliver whole prey to the nest, facilitating classification and quantification (Sonerud et al. 2014). In contrast, many species of galliforms, anseriforms and shorebirds lack parental feeding, as their chicks forage independently from an early age (Clutton-Brock 1991). In seabirds, monitoring food provisioning presents a particular challenge, especially in species where adults regurgitate semi-digested food stored in the crop or stomach, making prey identification and quantification difficult (e.g., Procellariiformes, Pelecaniformes, Sphenisciformes) (Olver 1978; Schreiber and Burger 2001; Ricklefs 1992; Wagner and Boersma 2019).

In seabird species that carry food internally, classic methods for monitoring food provisioning involve removing chicks from their nests immediately after being fed and inducing regurgitation through handling (i.e., stomach massage) or gastric lavage (i.e., water-offloading) (Weimerskirch et al. 2000; Phillips 2006). These procedures allow accurate assessment of meal size and diet composition but can be stressful for the animals (Votier et al. 2003). Less invasive methods involve weighing chicks before and after feeding (i.e., Giudici et al. 2017). However, this procedure which generally should be repeated several times a day (Hamer 1994) or at short time intervals to avoid underestimating meal size (Ramos and Pacheco 2003), may not only stress chicks but also affect their body condition and alter their behaviour (Larios et al. 2013). One way to address these issues is to place electronic scales under the nests (Sugishita et al. 2015). This remote weighing system can be programmed to record mass over short time intervals (e.g., 1.25 s) (Sugishita et al. 2015), minimising disturbance and maximising the amount and quality of the data obtained. Although this method has been used successfully, it has its limitations; electronic scales can only be used on certain types of nests (e.g., ground nests (Sugishita et al. 2017)), nests need to be handled (Grémillet et al. 1996) and sometimes modified, and estimating the mass of individual nestlings is complex for species that raise more than one chick (Lewis et al. 2004). In addition, factors such as meteorological conditions, faecal depositions, and the removal or addition of nest material can lead to unstable measurements (Prince and Watson 1984). Given these limitations, it is important to explore alternative technological methods that can estimate the amount of food that adult birds provide to their brood.

Technologies stemming from biologging (Campera et al. 2023; Watanabe and Papastamatiou 2023) now provide a broad spectrum of possibilities, and among these, accelerometers stand out (Brown et al. 2013). These compact sensors, easily attachable to animals, have become powerful and minimally invasive tools in animal behaviour research (Nathan et al. 2012; Fehlmann et al. 2017). They facilitate

the detection and quantification of behaviour by analysing acceleration patterns (Brown et al. 2013). The information recorded by accelerometers plays a dual role by indicating the animal's posture (i.e., via static acceleration) and the frequency and intensity of the movement associated with a particular activity (i.e., via dynamic acceleration) (Shepard et al. 2008). Furthermore, these sensors can estimate the costs related to certain activities by allowing calculation of dynamic body acceleration (DBA) (see Halsey et al. 2011). Accelerometers have been widely used across various bird species, enabling detailed studies of behaviours related to diving and flying. For instance, analysing acceleration patterns during prey capture has helped researchers estimate prey capture rates (Brisson-Curadeau et al. 2021) and explore the relationship between prey distribution and spatially explicit capture patterns (Carroll et al. 2014). Additionally, accelerometers facilitate the identification of different flight behaviours, which are crucial for understanding individual energy budgets (Sur et al. 2017).

In several seabird species, chick-feeding behaviour can be easily identified by distinct movements (Schreiber and Burger 2001; Nelson 2005). Gulls (Laridae), for example, regurgitate food on to the ground (Pierotti 1980), while albatrosses (Diomedeidae) inject a fluid mixture of oil and food fragments into the chicks' lower mandible (Johnstone et al. 1975; Nelson 1979). Penguins (Spheniscidae) and shags (Phalacrocoracidae) feed their chicks by regurgitating partially digested prey, which the chick retrieves by inserting its bill into the parent's bill and throat (Dunn 1975; Groscolas and Robin 2001). In the case of shags, adults exhibit conspicuous head and neck movements to expel regurgitated food to the chicks (Morrison et al. 1977; Giudici 2018).

A previous study by Del Caño et al. (2024) demonstrated that provisioning movements in the Imperial Shag (*Leucocarbo atriceps*) can be effectively identified using tri-axial accelerometers, revealing that these movements become more pronounced as chicks grow. This is because adults feed older chicks with larger and less processed prey items (i.e., whole fish rather than semi-liquid food that is provided to younger juveniles) (Dunn 1975), requiring more vigorous movements for transfer. Buildings upon these findings, the present study explores the extent to which head-mounted accelerometers on breeding Imperial shags can be used not only to identify but also to quantify food transfer to the brood. Our approach is based on a simple premise: the amount of food transferred correlates with the intensity and duration of the movements involved in regurgitation.



Table 1 Number of females instrumented with head accelerometers and number of chicks fed over three breeding seasons

Year	Instrumented adults	Chick age range (days)			
		≤ 7 days	8-14	15–21	
2019	12	6	6	3	
2021	16	5	12	6	
2022	6	0	6	3	
TOTAL	34	11	24	12	

# **Methods**

# Study area

Fieldwork was conducted at Punta León Imperial Shag colony (43°04'S, 64°29'W), Chubut, Argentina, between mid-November and mid-December of 2019, 2021 and 2022. This site hosts the largest and northernmost continental colony of Imperial shags on the Patagonian coast of Argentina, with over 6,000 nests, and has been the focus of several behavioural ecology studies over the past 30 years (Quintana et al. 2022).

#### **Nest selection**

A total of 40 nests were selected across different breeding seasons, including 14 nests in 2019, 18 nests in 2021, and 8 nests in 2022. During the study period, the clutch size of the selected nests varied from 1 to 3 chicks, meaning that our observations included nests with varying brood sizes. However, brood size was not a selection criterion as our focus was on the chick level. The key factors under study were chick age and parental actions (e.g., their movements),

rather than brood size. Chick age was estimated by measuring the tarsus length with a digital calliper (to the nearest 0.01 mm) at the time of capture for weighing (Svagelj et al. 2019; see below), and ranged from 1 to 21 days (Table 1).

#### **Animal instrumentation**

Adult females from each of the selected nests were instrumented with a triaxial accelerometer (Technosmart, Rome, Italy, 50 mm in length, 8 mm in width, 3 mm in height, 2 g weight) on the head (Fig. 1). The total weight of the device was less than 1% of the average adult female body mass, well below the recommended maximum of 3% (Kenward 2001). Accelerometers were set to record data at 50 Hz in each of the three orthogonal axes: surge (AccX, anteriorposterior axis), sway (AccY, the lateral axis), and heave (AccZ, dorso-ventral axis). We focused exclusively on females because they feed the chicks during the day (Harris et al. 2013), which made it easier to record their behaviours on video (see below). Adult females were distinguished from males by their vocalisations (males 'honk' and females 'hiss') (Malacalza and Hall 1988). Each female was gently removed from the nest using a specially designed hook to bring the animal closer to the handler without damaging the brood (Gómez-Laich et al. 2015). Once close to the handler, the shag was removed from the crook by grasping the neck behind the head with one hand and using the second hand to pull the wings up against the body (Gómez-Laich et al. 2015). Accelerometers were attached to the head feathers using Tesa® tape, following Wilson et al. (1997) (Fig. 1), taking particular attention that the devices were placed in the same position on each animal. In all cases, the



Fig. 1 Imperial Shag (Leucocarbo atriceps) equipped with a 2 g tri-axial accelerometer on the head. Photo: Andrea Benvenuti



instrumentation procedure was completed in less than 5 min and the birds were immediately returned to the nest. Since females leave the colony early in the morning to forage (Quintana et al. 2011; Harris et al. 2013), instrumentation took place in the afternoon (around 5 pm) of the day before the observations were performed (see below) and devices were left on the birds for 24 h. All birds carrying devices returned to the colony and resumed normal nest attendance and breeding behaviour.

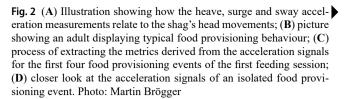
# Feeding events and the amount of food delivered by adults

During the first month of the chick-rearing period, breeding adults usually perform a single foraging trip per day, with females foraging in the morning and males in the afternoon (Quintana et al. 2011; Harris et al. 2013). Upon returning to the nest, females feed their chicks multiple times, during which a chick inserts its head into the adult's mouth (see definition below) (Giudici et al. 2017). Although females may conduct more than one feeding session in the afternoon (Giudici et al. 2017), this study focuses solely on the first feeding session, which began when the female arrived at the nest with food and started feeding a chick, and ended when no chicks had been fed for 15 min. It is important to note that during a feeding session, a single chick can receive food multiple times. To determine the specific provisioning acceleration signal associated with each chick in the clutch, the first feeding session of each instrumented female was recorded using a video camera (Sony DCRSR88). Cameras were placed between 2 and 3 m from the nest to minimize disturbance. To distinguish the chicks on film, nestlings were marked on the head and neck with non-toxic paint before the feeding session. These markings faded within 24 h (Giudici et al. 2017).

To quantify the amount of food transferred to the chicks during a feeding session, all the chicks in the brood were weighed twice using spring scales (Pesola® 100 g, 300 g, 500 g, and 1000 g). The first weighing was performed before the female's arrival (between 12 and 3 pm), and the second after the feeding session (see above). The difference between the initial and final weight was used to measure the amount of food transferred by the adult to each chick. Chicks from each brood were captured using a 1.5 m wooden pole with a small basket or cup at the end.

# **Data processing**

Video recordings were analysed using the free video player software Kinovea (Kinovea Creative Commons Attribution 2006). From the video images, it was possible to identify which chick was being fed on each occasion. The feeding



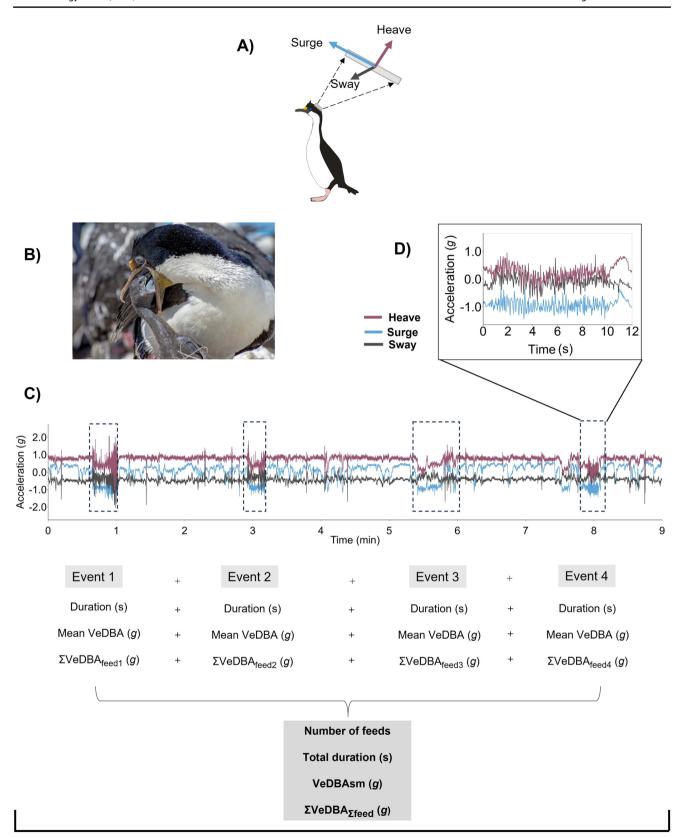
behaviour of each chick identified in the videos was then matched to the female's acceleration data using custom matching functions in the R software version 4.1.1 (R Core Team 2021) (Fig. 2). Once labelled, we determined the total acceleration of the translational movements: surge, sway, and heave from each provisioning acceleration signal. The static component of each acceleration axis was isolated by applying a running mean of 2 s following Shepard et al. (2008), while the dynamic component was calculated as the difference between raw and static acceleration. The dynamic component of each axis was used to compute the VeDBA following Qasem et al. (2012). VeDBA values were smoothed over 1 s to reduce the otherwise considerable variability in this metric (Wilson et al. 2019). From each chick food provisioning event, the duration and the mean VeDBA (an indicator of movement integrated in the three dimensions of space) were extracted (hereafter "event duration" and "mean event VeDBA" respectively) (Fig. 2C). The mean VeDBA value of each chick's food provisioning event was multiplied by the duration of the corresponding provisioning event to obtain the "total event VeDBA"  $(\Sigma VeDBA_{feedX}$  - an indicator of movement integrated over the three dimensions of space for feed event number X) (Fig. 2C). Finally, all feeding events identified for each chick during the first feeding session along with the extracted metrics were summed to obtain: (1) the total number of feeds (i.e. total number of times an adult regurgitated food to a chick), (2) the total duration of all feeds (total duration), (3) the mean VeDBA over the course of the feeding session (VeDBAsm), and (4) the summed mean VeDBA of the feeding session ( $\Sigma VeDBA_{\Sigma feed}$ , a proxy of the total movement involved in the provisioning behaviour of each chick during the first feeding session) (Fig. 2C).

# **Statistical analysis**

We examined the relationship between meal size with the number of feeds, total duration, VeDBAsm and  $\Sigma$ VeDBA $_{\Sigma}$ feed during the first feeding session. To do so, we used Generalized Linear Mixed Models (GLMMs) with a normal error distribution, where meal size was the response variable, and the number of feeds, total duration, VeD-BAsm,  $\Sigma$ VeDBA $_{\Sigma}$ feed, chick age and all possible two-way interactions were set as predictor variables. Nest identity and year were included as random intercepts in all models. Model assumptions were verified by graphical examination



Marine Biology (2025) 172:92 Page 5 of 11 92



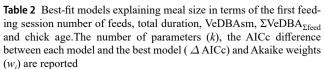
First feeding session

of residuals and by testing for normality (Shapiro-Wilk test). A power variance structure was incorporated as a function of chick age using the varPower function from the nlme package (Pinheiro et al. 2017) to model increasing residual variability with age. This structure was selected based on residual diagnostics that, revealed heteroscedasticity, allowing us to account for non-constant variance. To assess collinearity, the Pearson's correlation coefficient was calculated using the *cor* function, and variables which|r|<0.7 were retained in the full models (Fig. S1) (Harrison et al. 2018; Scharf et al. 2021). Due to collinearity, the following pairs of explanatory variables were never included together in the same candidate model:  $\Sigma VeDBA_{\Sigma feed}$  and VeDBAsm, number of feeds and VeDBAsm, and  $\Sigma \text{VeDBA}_{\Sigma \text{feed}}$  and total duration (Fig. S1, Table S1). In total, we evaluated 29 models explaining meal size (Supplementary information, Table S1). The corrected Akaike Information Criterion (AICc), AICc weight  $(w_i)$  and  $\Delta$  AICc values between models were obtained using the *nlme* and *MuMin* packages (Bartón 2019) (Supplementary information, Table S2). Models were ranked according to their  $\Delta$  AICc values, with the lowest  $\Delta$  AICc model selected as the best predictor of meal size. However, if multiple competing models fell within  $\Delta$  AICc  $\leq 2$  of the top ranked model, the most parsimonious one (i.e., the one that included the fewest uninformative parameters) was selected for inference (Lehikoinen et al. 2021). A parameter was considered uninformative if the 85% confidence interval included zero (Arnold 2010).

Finally, we performed a 5-fold cross-validation analysis (Gareth et al. 2013) to evaluate model performance. For this, the dataset was divided into five subsets (folds) of similar size, with four folds used for training and the remaining fold for testing. This process was repeated five times, ensuring that each fold served as the test set once. Model predictions were compared with observed meal size using Mean Squared Error (MSE) and the coefficient of determination (r²) (see Supplementary Information). All statistical analyses were conducted using R software version 4.1.1 (R Core Team 2021).

# Results

Of the 40 nests studied, data from six were discarded due to the absence of meal size records, as measurements could not be obtained due to operational constraints. Consequently, data were collected from a total of 378 food provisioning acceleration signals from 34 adult female Imperial shags (Table 1). Of these signals, 16% were recorded during periods when females were feeding chicks less than 7 days old, 59% while feeding chicks between 8 and 14 days old, and 25% while feeding chicks aged between 15 and 21 days



Response variable	Fixed effects	k	$\Delta$ AICc	Wi
Meal size	VeDBAsm*Age	8	0.00	0.902
	Total duration +VeDBAsm*Age	9	6.21	0.040
	Number of feeds*Age	8	6.64	0.033

Bold font indicates the model with the best fit according to AICc

**Table 3** Parameter estimates for the best-fit model describing the relationship between imperial shags meal size during the first feeding session and variables derived from adult female food provisioning acceleration signals and chick age

Model	Coefficients	Estimate (±	t-value	<i>p</i> -value
		SE)		
Meal size~	Intercept	4.978	1.634	0.1123
VeDBAsm*Age		(3.046)		
	VeDBAsm	-9.948	-3.702	0.0041
		(2.687)		
	Age	2.925	4.430	0.0013
		(0.660)		
	VeDBAsm: Age	1.317	4.296	0.002
		(0.306)		

Bold font indicates statistically significant results (p < 0.05)

(Table 1). In total, we obtained information on meal size from 47 chicks fed during the first feeding session (Table 1). The total duration of the first feeding session was on average  $23 \pm 18 \text{ min } (N=34)$ .

The best model explaining the variation in meal size included both VeDBAsm and chick age ( $\Delta$  AICc = 0,  $w_i$ = 0.902, Table 2). Meal size was negative associated with VeDBAsm (head movement intensity,  $t_{10}$ = -3.702; P= 0.0041) (Table 3; Fig. 3) and, increased with chick age ( $t_{10}$ = 4.43; P= 0.0013) (Table 3; Fig. 3). Additionally, the interaction between VeDBAsm and age had a significant effect on meal size ( $t_{10}$ = 4.296; P= 0.002); Table 3; Fig. 3). As shown in Fig. 3, the positive interaction between VeDBAsm and age (1.32; Table 2) indicated that the effect of VeDBAsm on meal size varied with age. For younger chicks, an increase in adult movement intensity did not necessarily result in larger meal size. In contrast, for older chicks (> 7 days), more vigorous provisioning movements by the adult lead to a larger meal size.

The cross-validation results indicate that the model captures general patterns in the data, with some variability between subsets (Supplementary Information, Fig. S2, S3). The determination coefficients (r²) for each fold ranged from 0.4 to 0.8, highlighting variation in model fit across subsets (Supplementary Information Fig. S2). Overall, results showed a positive trend between predicted and observed meal size, though some folds exhibited greater dispersion



Marine Biology (2025) 172:92 Page 7 of 11 92

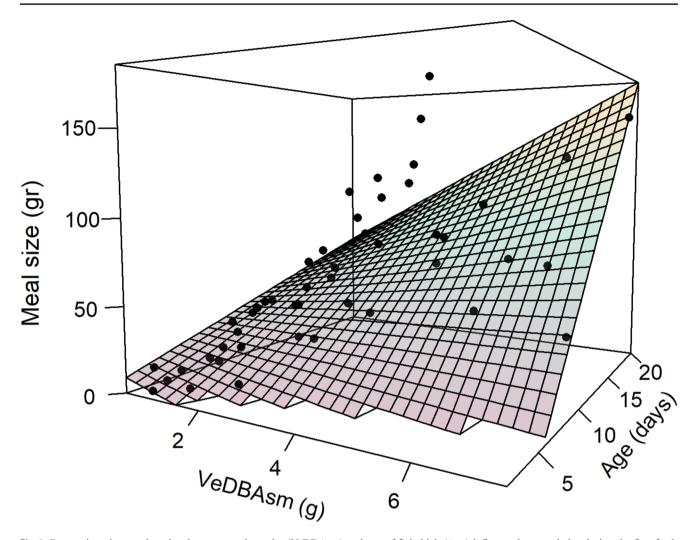


Fig. 3 Regression plane on how head movement intensity (VeDBAsm) and age of fed chick (Age) influenced on meal size during the first feeding session. The black dots represent the observed values. The regression plane of the 3D figure was clipped to display only the plausible values

(Fig. S2). The mean square error (MSE) varied across folds (Fig. S3), with lower values in folds 2, 3 and 5 and higher values in folds 1 and 4, suggesting that certain data subsets better captured the relationship between adult behaviour and meal size.

# Discussion

This study highlights the potential utility of head acceleration metrics for quantifying food delivered by adult Imperial shags to their offspring, particularly in older chicks (> 7 days), where feeding movements are more pronounced. Our findings suggest that, as chicks age, adults transfer more food. In general terms, the model captures general patterns in the data, with variability observed across the folds in the cross-validation likely due to differing numbers of younger chicks in each fold.

In older chicks, more vigorous regurgitation movements by the female resulted in larger meal sizes, a relationship not observed in younger chicks. Among the accelerationderived metrics assessed, VeDBAsm was the most effective predictor of meal size. The increase in the quantity of food delivered by females to their chicks as they grow aligns with previous studies on Imperial shags and other seabird species (Quillfeldt and Peter 2000; Low et al. 2012; Giudici et al. 2017). This trend was expected, as the energy demands of chicks rise with age (Dunn 1975, 1976). To meet these growing energy requirements, adults may feed their chicks more frequently and/or provide larger and more energy rich prey (Wiebe and Slagsvold 2014; Ibarra et al. 2022). As our results indicate, female Imperial shags apparently do not increase the quantity of food transferred by increasing the number of regurgitation events within a feeding session. This could be because fewer regurgitations may deliver a larger total food volume compared to multiple smaller transfers. Additionally, not every chick beak insertions into the



adult's mouth necessarily results in successful food transfers (Wagner and Boersma 2019).

VeDBAsm, proved to be a more effective predictor of meal size than  $\Sigma VeDBA_{\Sigma feed}$  (the combination of duration and intensity of the head movement) suggesting that the intensity of adult head movement (i.e., how vigorously adults move their heads) during food transfer is a strong indicator of provisioning success. Notably, VeDBAsm exhibited greater variability when feeding older chicks, likely due to differences in the digestibility of food being transferred (Olver 1984; Goutner et al. 1997). At Punta León colony, females primarily feed chicks with Raneya brasiliensis during the early development stage (less than 15 days) (Ibarra et al. 2022). At this stage, females may provide semi-liquid food, which requires less vigorous head movements for transfer (Del Caño et al. 2024). It is important to note that anatomical constraints in small chicks' oral cavity prevent them from ingesting excessively large food portions (Klasing 1999). As chicks grow, females incorporate larger prey, such as Merluccius hubbsi, into their diet (Ibarra et al. 2022), which may require more vigorous movements for successful transfer.

The proposed approach for estimating the amount of food transferred by adults to their brood has the potential to be applied to any seabird species whose provisioning behaviour involves distinct, identifiable movements and allows for the proper attachment of an accelerometer on the body part that best captures those movements. Species with long necks and a provisioning behaviour involving beak-tobeak contact, such as boobies and gannets (family Sulidae), and pelicans (family Pelecanidae) (Kirkham 1982; Johnsgard 1993), would be particularly suitable for this method. Additionally, seabird species without long necks but with similar provisioning behaviours such as those in families Spheniscidae, Phaethontidae and Fregatidae (Howell and Bartholomew 1969; Schreiber and Burger 2001; Wagner and Boersma 2019), could also be viable candidates. In all these species, accelerometers could be used to continuous monitor behaviour, documenting food provisioning activity at various times of day, even in situations where direct observation is challenging. Furthermore, accelerometers eliminate the need for the observer to maintain a specific position, enabling accurate identification of food delivery even when the adult or chick is out of sight. For extended monitoring, if foraging trip schedules are well known (as in Punta León shags), accelerometers could be programmed to record only land-based behaviours, optimizing battery life. In our study, devices were attached to adults' heads using only Tesa tape, but for multi-day recordings, additional reinforcement may be needed to ensure secure attachment.

It should be noted that the proposed methodology may not be applicable to species such as puffins and terns which carry fish in their beaks and offer whole prey items directly to their chicks (Corkhill 1973; Hopkins 1972). In these cases, food transfer involves minimal head or body movement, making it difficult to detect feeding events using accelerometry. While accelerometers offer many advantages, it is important to highlight some considerations. These devices are small and lightweight, allowing for quick and standardized placement, which helps minimize variations in sensor positioning and ensures consistent measurements. However, their deployment requires capturing, attaching, and subsequently releasing the animal, which must be carefully managed to minimize stress and potential impacts on the individual. Additionally, processing acceleration data involves handling large volumes of information to accurately interpret movements and distinguish between different behaviours. These aspects can pose challenges, particularly in studies requiring long-term monitoring or large sample sizes. Understanding these limitations is crucial for researchers seeking to adopt this methodology. Finally, it is important to note, that the lack of video recording of the feeding session precludes the possibility of determining which chick in a multi-chick brood is being fed by the instrumented adult. This limitation can be overcome by simultaneously instrumenting both adults and chicks allowing for the identification of the fed chick through the analysis of its acceleration profile. However, in the absence of video recordings, it is necessary to first identify food provisioning signals from accelerometer data to extract feeding metrics. This step can be particularly challenging for younger chicks (see Del Caño et al. 2024).

In conclusion, the findings of our study have significant implications for methodological advancements in the ecological research of shags and their relatives, with potential applications extending to other seabird species. Our findings also hold far-reaching implications for the study of parental behaviour, evolutionary ecology, and bird conservation. However, questions regarding the broader applicability of these findings remain unanswered, particularly concerning the need to address individual variation, optimize logger deployment, and validate the method in other species. Our results suggest that this approach is currently most effective for older chicks (> 7 days) of Imperial shags, as identifying provisioning events and quantifying food provisioning in younger chicks remains challenging. Nonetheless, the proposed methodology offers a viable and less invasive alternative to traditional methods, such as chick weighing or induced regurgitation (Wagner and Boersma 2019; Phillips 2006). In particular, it provides an opportunity to investigate the role of the sexes in food provisioning during the chickrearing period in Imperial shags an issue not addressed in previous studies (Giudici et al. 2017). Future research could investigate sex differences in food provisioning and the role of parental foraging effort, as accelerometer data on food



Marine Biology (2025) 172:92 Page 9 of 11 92

provisioning behaviour can be complemented with foraging trip data (Laich et al. 2008), allowing for an examination of the relationship between parental foraging effort and the amount of food delivered.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00227-025-04654-z.

Acknowledgements We would like to express our gratitude to Swansea University for providing MDC with the opportunity to utilise their facilities. That experience proved to be a crucial element in the advancement of a significant portion of this work. We would like to express our gratitude to La Chola, Miguel and Estancia El Pedral for their valuable assistance in various aspects of this research. Additionally, we would like to express our gratitude to the Instituto de Biología de Organismos Marinos (IBIOMAR-CONICET) for the institutional and logistical support. Finally, we sincerely appreciate the valuable feedback provided by the reviewers, whose insightful comments and suggestions have greatly contributed to improving this manuscript.

Author contributions AGL and FQ conceptualized the initial research question. AGL and FQ conceived the study and the methodology. AGL and MDC collected the data. MDC completed statistical analysis with the help of AGL, FQ and RPW. MDC wrote the original draft and the manuscript with support from AGL and FQ. All authors contributed to the reviewing and editing. FQ and GDO provided resources. AGL, FQ and RPW supervised the project. All authors have read and approved the final version of the paper.

**Funding** This work was supported by a grant from the National Agency for the Promotion of Science and Technology of Argentina (grant PICT 2017–1996 to AGL), and by two awards, one from the Association of Field Ornithologists and the other from Aves Argentinas to MDC.

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

#### **Declarations**

Competing interests The authors declare no conflict of interest.

Ethical approval All handling procedures were approved by the Dirección de Fauna y Flora Silvestre (Permit 101/22-DFyFS), the Ministerio de Turismo y Áreas Protegidas of the Province of Chubut (Permits 47/19 and 63/21-SsCyAP) and the Comité Institucional para el Uso de Animales de Experimentación (CICUAE CCT CENPAT CONICET) (Resolution 6/2021).

Consent to participate Not applicable.

Consent to Publication Not applicable.

# References

Arnold TW (2010) Uninformative parameters and model selection using Akaike's information criterion. J Wildl Manag 74(6):1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

Bartón K (2019) MuMIn: Multi-Model Inference. R package version 1.43.6. Available at: https://CRAN.R-project.org/package=MuM In. Accessed January 15, 2020

- Brisson-Curadeau É, Handrich Y, Elliott KH, Bost CA (2021) Accelerometry predicts prey-capture rates in the deep-diving King Penguin *Aptenodytes patagonicus*. Mar Biol 168:1–10
- Brown DD, Kays R, Wikelski M, Wilson R, Klimley AP (2013)
  Observing the unwatchable through acceleration logging of animal behavior. Anim Biotelem 1:1–16. https://doi.org/10.1186/2050-3385-1-20
- Campera M, Chimienti M, Nekaris KAI (2023) Applications of accelerometers and other Bio-Logging devices in captive and wild animals. Animals. https://doi.org/10.3390/ani13020222
- Carroll G, Slip D, Jonsen I, Harcourt R (2014) Supervised accelerometry analysis can identify prey capture by Penguins at sea. J Exp Biol 217(24):4295–4302
- Clutton-Brock TH (1991) The evolution of parental care, vol 10. Princeton University Press, Princeton
- Corkhill P (1973) Food and feeding ecology of Puffins. Bird Study 20(3):207–220. https://doi.org/10.1080/00063657309476382
- Del Caño M, Quintana F, Dell'Omo G, Gómez-Laich A (2024) Triaxial accelerometry allows to determine parental food provisioning behaviour in a marine bird. Avian Res 15:100194. https://doi. org/10.1016/j.avrs.2024.100194
- Dunn EH (1975) Caloric intake of nestling double-crested cormorants. Auk 92(3):553–565. https://www.jstor.org/stable/4084609
- Dunn EH (1976) Development of endothermy and existence energy expenditure of nestling Double-crested Cormorants. The Condor 78(3):350–356.
- Fehlmann G, O'Riain MJ, Hopkins PW, O'Sullivan J, Holton MD, Shepard EL, King AJ (2017) Identification of behaviours from accelerometer data in a wild social primate. Anim Biotelem 5:1–11. https://doi.org/10.1186/s40317-017-0121-3
- Forbes S, Glassey B (2000) Asymetric sibling rivalry and nestling growth in red-winged Blackbirds (*Agelaius phoeniceus*). Behav Ecol Sociobiol 48:413–417. https://doi.org/10.1007/s002650000 239
- Gangloff B, Wilson KJ (2004) Feeding frequency, meal size and chick growth in Pycroft's petrel (*Pterodroma pycrofti*): Preparing for chick translocations in Pterodroma species. Notornis 51:26–32
- Gareth J, Witten D, Hastie T, Tibshirani R, Taylor J (2023) Resampling Methods. In: An Introduction to Statistical Learning. Springer Texts in Statistics. Springer, Cham. https://doi.org/10.1007/978-3-031-38747-0 5
- Giudici PI (2018) Reducción de nidada en el cormorán imperial (*Phalacrocorax atriceps*): causas próximas y últimas de una estrategia reproductiva. Dissertation, Universidad Nacional del Comahue, Argentina
- Giudici PI, Quintana F, Svagelj WS (2017) The role of hatching asynchrony in a seabird species exhibiting obligate brood reduction. Waterbirds 40(3):221–232. https://doi.org/10.1675/063.040.0304
- Gómez-Laich A, Yoda K, Zavalaga C, Quintana F (2015) Selfies of imperial cormorants (*Phalacrocorax atriceps*): what is happening underwater? PLoS ONE 10(9):e0136980. https://doi.org/10.1371/journal.pone.0136980
- Goutner V, Papakostas G, Economidis PS (1997) Diet and growth of great cormorant (*Phalacrocorax carbo*) nestlings in a mediterranean estuarine environment (Axios delta, Greece). Isr J Ecol Evol 43(2):133–148. https://doi.org/10.1080/00212210.1997.10 688898
- Granadeiro JP, Burns MD, Furness RW (1999) Food provisioning to nestling shearwaters: why parental behaviour should be monitored? Anim Behav 57(3):663–671. https://doi.org/10.1006/anbe.1998.0992
- Grémillet D, Dey R, Wanless S, Harris MP, Regel J (1996) Determining food intake by great cormorants and European shags



92 Page 10 of 11 Marine Biology (2025) 172:92

- with electronic balances (Determinando Las caracteristicas de ingestión de *Phalacrocorax carbo y P. aristotelis* Con Balanzas electrónicas). J Field Ornithol 67(4): 637–648 https://www.jstor.org/stable/4514168
- Groscolas R, Robin JP (2001) Long-term fasting and re-feeding in Penguins. Comp Biochem Physiol Mol Integr Physiol 128(3):643–653
- Grundel R (1987) Determinants of nestling feeding rates and parental investment in the mountain Chickadee. Condor 89(2):319–328. h ttps://doi.org/10.2307/1368484
- Halsey LG, Shepard EL, Wilson RP (2011) Assessing the development and application of the accelerometry technique for estimating energy expenditure. Comp Biochem Physiol A: Mol Integr Physiol 158(3):305–314. https://doi.org/10.1016/j.cbpa.2010.09.002
- Hamer KC (1994) Variability and stochasticity of meal size and feeding frequency in the little sheanvater *Puffinus assimilis*. Ibis 136(3):271–278. https://doi.org/10.1111/j.1474-919X.1994.tb01 095.x
- Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CE, Robinson BS, Hodgson DJ, Inger R (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology. Peer J 6:e4794. https://doi.org/10.7717/peerj.4 794
- Harris S, Raya Rey A, Phillips RA, Quintana F (2013) Sexual segregation in timing of foraging by imperial shags (*Phalacrocorax atriceps*): is it always ladies first? Mar Biol 160:1249–1258. https://doi.org/10.1007/s00227-013-2177-9
- Hopkins CD, Wiley RH (1972) Food parasitism and competition in two Terns. Auk 89(3):583–594. https://www.jstor.org/stable/408 4258
- Howell TR, Bartholomew GA (1969) Experiments on nesting behavior of the Red-tailed tropicbird, *Phaethon rubricauda*. Condor 71(2):113–119
- Ibarra C, Marinao C, Suárez N, Kasinsky T, Yorio P (2022) Patterns of sexual segregation in the use of trophic resources in breeding imperial cormorants. Mar Biol 169(12):154. https://doi.org/10.10 07/s00227-022-04143-7
- Johnsgard PA (1993) Cormorants, darters, and pelicans of the world. Smithsonian Institution, Washington D.C.
- Johnstone GW, Milledge D, Dorward DF (1975) The White-capped Albatross of Albatross Island: numbers and breeding behaviour. Emu 75(1):1–11. https://doi.org/10.1071/MU9750001
- Kacelnik A, Cotton PA, Stirling L, Wright J (1995) Food allocation among nestling Starling: sibling competition and the scope of parental choice. Proc Roy Soc Lond Ser B Biol Sci 259(1356):259–263. https://doi.org/10.1098/rspb.1995.0038
- Kenward RE (2001) A manual for wildlife radio tagging. Academic Kinovea (2006) Kinovea v. 0.8.15 for Windows. Kinovea Paris France. Accessed 10 March 2014. http://www.kinovea. Org
- Kirkham IR, Montevecchi WA (1982) Growth and thermal development of Northern Gannets (Sula bassanus) in Atlantic Canada. Col Waterbirds: 66–72
- Klasing KC (1999) Avian Gastrointestinal anatomy and physiology. Sem Min Avian Exot Pet Med 8(2):42–50
- Laich AG, Wilson RP, Quintana F, Shepard EL (2008) Identification of imperial cormorant *Phalacrocorax atriceps* behaviour using accelerometers. Endanger Species Res 10:29–37. https://doi.org/10.3354/esr00091
- Larios DF, Rodríguez C, Barbancho J, Baena M, Leal MÁ, Marín J, León C, Bustamante C (2013) An automatic weighting system for wild animals based in an artificial neural network: how to weigh wild animals without causing stress. Sensors 13(3):2862–2883. h ttps://doi.org/10.3390/s130302862
- Lehikoinen P, Tiusanen M, Santangeli A, Rajasärkkä A, Jaatinen K, Valkama J, Virkkala R, Lehikoinen A (2021) Increasing protected

- area coverage mitigates climate-driven community changes. Biol Conserv 253:108892. https://doi.org/10.1016/j.biocon.2020.1088
- Lewis S, Hamer KC, Money L, Griffiths R, Wanless S, Sherratt TN (2004) Brood neglect and contingent foraging behavior in a pelagic seabird. Behav Ecol Sociobiol 56:81–88. https://doi.org/10.1007/s00265-004-0762-0
- Low M, Makan T, Castro I (2012) Food availability and offspring demand influence sex-specific patterns and repeatability of parental provisioning. Behav Ecol 23(1):25–34. https://doi.org/10.1093/beheco/arr145
- Malacalza VE, Hall MA (1988) Sexing adult King cormorants (*Phalacrocorax albiventer*) by discriminant analysis. Colon Waterbirds 11:32–37. https://www.jstor.org/stable/1521167
- Morrison ML, Shanley E Jr, Slack RD (1977) The food of nestling olivaceous cormorants. Southwest Nat 22(3):321–326. https://www.jstor.org/stable/30054799
- Nathan R, Spiegel O, Fortmann-Roe S, Harel R, Wikelski M, Getz WM (2012) Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. J Exp Biol 215(6):986–996. https://doi.org/10.1242/jeb.058602
- Nelson JB (1979) Seabirds: their biology and ecology. Hamlyn's, London
- Nelson JB (2006) Pelicans, cormorants, and their relatives. Pelecanidae, Sulidae, Phalacrocoracidae, Anhingidae, fregatidae, Phaethontidae. OUP, Oxford
- Olver MD (1984) Breeding biology of the Reed cormorant. Ostrich 55(5):133–140. https://doi.org/10.1080/00306525.1984.9633622
- Phillips RA (2006) Efficacy and effects of diet sampling of Albatross chicks. Emu-Austral Ornithol 106(4):305–308. https://doi.org/10 .1071/MU06035
- Pierotti R (1980) Spite and altruism in gulls. Am Nat 115(2):290–300. https://doi.org/10.1086/283561
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2017) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–131. Available at: https://CRAN.R-project.org/package=nlm e. Accessed January 15,2020
- Price K, Ydenberg R (1995) Begging and provisioning in broods of asynchronously hatched yellow-headed Blackbird nestlings. Behav Ecol Sociobiol 37:201–208. https://doi.org/10.1007/BF0 0176718
- Qasem L, Cardew A, Wilson A, Griffiths I, Halsey LG, Shepard EL, Gleiss AC, Wilson R (2012) Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? PLoS ONE 7(2):e31187. https://do i.org/10.1371/journal.pone.0031187
- Quillfeldt P, Peter HU (2000) Provisioning and growth in chicks of Wilson's storm-petrels (*Oceanites oceanicus*) on King George Island, South Shetland Islands. Pol Biol 23:817–824. https://doi.org/10.1007/s003000000158
- Quintana F, Wilson R, Dell'Arciprete P, Shepard E, Laich AG (2011) Women from Venus, men from Mars: inter-sex foraging differences in the imperial cormorant *Phalacrocorax atriceps* a colonial seabird. Oikos 120(3):350–358. https://doi.org/10.1111/j.16 00-0706.2010.18387.x
- Quintana F, Wilson R, Prandoni N, Svagelj WS, Gómez-Laich A (2022) Long-Term ecology studies in Patagonian seabirds: A review with the imperial cormorant as a case study. Global change in Atlantic coastal patagonian ecosystems. Natural and social sciences of patagonia. Springer, Cham. https://doi.org/10.1007/978-3-030-8 6676-1 10
- Ramos JA, Pacheco C (2003) Chick growth and provisioning of surviving and nonsurviving White-tailed tropicbirds (*Phaethon lepturus*). Wilson Bull 115(4):414–422. https://doi.org/10.1676/03-052



Marine Biology (2025) 172:92 Page 11 of 11 92

R Core Team (2021) R: a Language and environment for statistical computing. Vienna: R foundation for statistical computing. http://www.R-project.org

- Ricklefs RE (1992) The roles of parent and chick in determining feeding rates in Leach's storm-petrel. Anim Behav 43(6):895–906
- Safriel UN (1981) Social hierarchy among siblings in broods of the oystercatcher *Haematopus ostralegus*. Behav Ecol Sociobiol 9:59–63. https://doi.org/10.1007/BF00299854
- Scharf HM, Hauber ME, Mommer BC, Hoover JP, Schelsky WM (2021) The effect of avian brood parasitism on physiological responses of host nestlings. Oecologia 195:861–872. https://doi.org/10.1007/s00442-021-04888-w
- Schreiber EA, Burger J (2001) Biology of marine birds. CRC Press LL, Florida
- Schwagmeyer PL, Mock DW (2008) Parental provisioning and offspring fitness: size matters. Anim Behav 75(1):291–298
- Shepard EL, Wilson RP, Quintana F, Laich AG, Liebsch N, Albareda DA, Halsey LG, Gleiss A, Morgan DT, Myers AE et al (2008) Identification of animal movement patterns using tri-axial accelerometry. Endanger Species Res 10:47–60. https://doi.org/10.3354/esr00084
- Sonerud GA, Steen R, Løw LM, Røed LT, Skar K, Selås V, Slagsvold T (2014) Evolution of parental roles in raptors: prey type determines role asymmetry in the Eurasian kestrel. Anim Behav 96:31–38
- Sugishita J, McKenzie M, Torres LG, Seddon PJ (2017) Automated techniques for measuring meal size in great albatrosses. N Z J Ecol 41(1):120–125. https://www.jstor.org/stable/26198790
- Sugishita J, Torres LG, Seddon PJ (2015) A new approach to study of seabird-fishery overlap: connecting chick feeding with parental foraging and overlap with fishing vessels. Global Ecol Conserv 4:632–644. https://doi.org/10.1016/j.gecco.2015.11.001
- Sur M, Suffredini T, Wessells SM, Bloom PH, Lanzone M, Blackshire S, Srisarguru S, Katzner T (2017) Improved supervised classification of accelerometry data to distinguish behaviors of soaring birds. PLoS ONE 12(4):e0174785
- Svagelj WS, Quintana F (2007) Sexual size dimorphism and sex determination by morphometric measurements in breeding imperial shags (*Phalacrocorax atriceps*). Waterbirds 30(1):97–102
- Thaxter CB, Daunt F, Hamer KC, Watanuki Y, Harris MP, Grémillet Peters G, Wanless S (2009) Sex-specific food provisioning in a monomorphic seabird, the common guillemot *Uria aalge*: nest defence, foraging efficiency or parental effort? J Avian Biol 40(1):75–84. https://doi.org/10.1111/j.1600-048X.2008.04507.x

- Trivers RL (1974) Parent-Offspring conflict. Am Zool 14(1):249–264. https://doi.org/10.1093/icb/14.1.249
- Votier SC, Bearhop S, MacCormick A, Ratcliffe N, Furness RW (2003) Assessing the diet of great Skuas, *Catharacta skua*, using five different techniques. Pol Biol 26:20–26. https://doi.org/10.10 07/s00300-002-0446-z
- Wagner EL, Boersma PD (2019) Food allocation and feeding behaviours of Magellanic Penguin, *Spheniscus magellanicus*, adults and chicks. Anim Behav 148:161–168. https://doi.org/10.1016/j.anbehav.2018.12.008
- Watanabe YY, Papastamatiou YP (2023) Biologging and biotelemetry: tools for Understanding the lives and environments of marine animals. Annu Rev Anim Biosci 11(1):247–267. https://doi.org/10.1146/annurev-animal-050322-073657
- Weimerskirch H, Prince PA, Zimmermann L (2000) Chick provisioning by the Yellow-nosed Albatross *Diomedea chlororhynchos*: response of foraging effort to experimentally increased costs and demands. Ibis 142(1):103–110. https://doi.org/10.1111/j.1474-919X.2000.tb07689.x
- Wiebe KL, Slagsvold T (2014) Prey size increases with nestling age: are provisioning parents programmed or responding to cues from offspring? Behav Ecol Sociobiol 68:711–719. https://doi.org/10.1007/s00265-014-1684-0
- Wilson RP, Börger L, Holton MD, Scantlebury DM, Gómez-Laich A, Quintana F, Rosell F, Graf PM, Williams H, Gunner R et al (2019) Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. J Anim Ecol 89(1):161–172. https://doi.org/10.1111/1365-2656.13040
- Wilson RP, Pütz K, Peters G, Culik B, Scolaro JA, Charrassin JB, Ropert-Coudert Y(1997) Long-term attachment of transmitting and recording devices to Penguins andother seabirds. Wildl Soc Bull25(1):101–106

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.

