Assessing meal size in seabirds through head movement dynamics

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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 minutes. 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

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 et al. 2004; Low and Castro 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 (Prince and Watson 1984; 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 (Reid et al. 1999), and estimating the mass of individual nestlings is complex for species that raise more than one chick (Prince and Watson 1984; 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. 2017). 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 2006). 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 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; Spurr 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 finding, 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.

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 (Svagelj and Quintana 2007), 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, anterior-posterior 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; Svagelj and Quintana 2007). 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 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 minutes. 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 hours (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. 1). 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. 1C). 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" ($\Sigma \mathrm{VeDBA}_{\mathrm{feedX}}$ - an indicator of movement integrated over the three dimensions of space for feed event number X) (Fig. 1C). 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 ($\Sigma \mathrm{VeDBA}_{\Sigma \mathrm{feed}}$, a proxy of the total movement involved in the provisioning behaviour of each chick during the first feeding session) (Fig. 1C).

Statistical analysis

We examined the relationship between meal size with the number of feeds, total duration, VeDBAsm and $\Sigma \mathrm{VeDBA}_{\Sigma \mathrm{feed}}$ 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, VeDBAsm, $\Sigma \mathrm{VeDBA}_{\Sigma \mathrm{feed}}$, 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 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: $\Sigma \mathrm{VeDBA}_{\Sigma \mathrm{feed}}$ and VeDBAsm, number of feeds and VeDBAsm, and $\Sigma \mathrm{VeDBA}_{\Sigma \mathrm{feed}}$ 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 ΔAICc values between models were obtained using the *nlme* and *MuMin* packages (Bartón, 2019) (Supplementary information, Table S2). Models were ranked according to their ΔAICc values, with the lowest ΔAICc model selected as the best predictor of meal size. However, if multiple competing models fell within $\Delta \mathrm{AICc} \leq 2$ 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 (r^2) (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 to 21 days (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 ± 18 min (N=34).

The best model explaining the variation in meal size included both VeDBAsm and chick age (ΔAICc=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, Figure 3) and, increased with chick age (t_{10}= 4.43; P= 0.0013) (Table 3, Figure 3). Additionally, the interaction between VeDBAsm and age had a significant effect on meal size (t_{10}= 4.296; P= 0.002); Table 3, Figure 3). As shown in Figure 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 (r^2) 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 (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 acceleration-derived 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. 2011; 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 $\Sigma \mathrm{VeDBA}_{\Sigma \mathrm{feed}}$ (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 (less than 15 days) development stage (> 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-to-beak 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 chick-rearing 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 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.

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Competing interests

The authors declare no conflict of interest.

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

Data Availability

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

Ethics 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 publish

Not applicable

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Figure captions

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

Fig.2. A) Illustration showing how the heave, surge and sway acceleration measurements relate to the shag's head movements; B) picture showing an adult displaying typical food provisioning behaviour; C) process of extracting the metrics derived from the acceleration signals for the first four food provisioning events of the first feeding session; D) closer look at the acceleration signals of an isolated food provisioning event. Photo: Martin Brögger

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.

Tables

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

		Chick age range (days)		
Year	Instrumented adults	≤ 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**

Table 2: Best-fit models explaining meal size in terms of the first feeding session number of feeds, total duration, VeDBAsm, ΣVeDBA$_{\Sigma\text{feed}}$ and chick age. The best model for inference is shown in bold. The number of parameters (*k*), the AICc difference between each model and the best model (ΔAICc) and Akaike weights (w_i) are reported.

Response variable	Fixed effects	*k*	ΔAICc	w_i
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

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