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MONITORING JAW MOVEMENTS: A CUE TO FEEDING ACTIVITY

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ABSTRACT

We investigated the potential of a recently-developed data logger that monitors jaw movements using a magnet/Hall sensor combination to identify features that characterize prey ingestion. Experiments were conducted on eleven captive animal species of mammals, birds and turtles, with carnivorous and herbivorous feeding habits, exploiting either marine or terrestrial environments. Following calibration, the timing of prey ingestion was accurately detected in all instances but food manipulation prior to swallowing led to a large interspecific variability in jaw opening angle over time. Pros and cons of the system are given together with an assessment of the applicability of such a tool for ecological studies on free-ranging animals. Overall, the system proved promising for estimation of the quantity and quality of the food.

I. INTRODUCTION

Assessment of the feeding activity of free-ranging animals is important for modelling energy flux in ecosystems (ELTON, 1927). For example, assessments of the attributes of ruminant diets are necessary to fully understand pasture–animal relationships and to manage grassland systems (COATES and PENNING, 2000). However, for many species, feeding behaviour cannot be observed directly or cannot be quantified by direct measurements. This is especially true in the case of free-ranging individuals foraging in ecosystems that are difficult to access such as marine environments (KOOYMAN *et al.*, 1992), deserts (MEYERS, 1996), forests, as well as for nocturnal feeders.

Many techniques have been developed to investigate feeding habits of non-disturbed animals. These techniques differed primarily in the questions asked. Overall, we can separate studies into those that aim to investigate diet composition and those designed to determine the occurrence of food intake over time. Early studies of the diet composition of free-ranging animals consisted of the analysis of feces and its microhistological remnants (*e.g.* SPARKS and MALECHEK, 1968) but there is little reliable information to be gained by this approach (FURNESS and MONAGHAN, 1987; REYNOLDS and AEBISCHER, 1991; CIUCCI *et al.*, 1996; BAUBET *et al.*, 1997). A similar method consists of collecting the stomach content of dead animals, *e.g.* individuals shot during the hunting season (BAUBET, 1998). Regurgitation of the stomach contents using emetics (DAHLGREN, 1982), oesophageal or rumen fistulation in herbivores (HOLECHEK *et al.*, 1982; STEVENS *et al.*, 1985) or stomach pumping (WILSON, 1984) have obviated the necessity of killing animals but, ultimately, all these methods are subject to bias (BÉDARD, 1976; CROXALL and PRINCE, 1980; CARSS, 1995).

Rate of food ingestion is not addressed by these techniques (WILSON *et al.*, 1985; JACKSON, 1992). Recently, telemetric monitoring or the logging of feeding habits have been developed to the point that information on the timing of food consumption in the wild and the mass of ingested food can be determined *in situ*. These techniques are promising when dealing with animals that forage in remote areas where direct observation is difficult, *i.e.* marine endotherms feeding on ectothermic prey. Temperature records from sensors either located in the stomach (WILSON *et al.*, 1992) or in the oesophagus (ROPERT-COUDERT *et al.*, 2000) have provided substantial information on the depth (CHARRASSIN *et al.*, 2000) and the time (WILSON *et al.*, 1993) at which prey were ingested, and provided information on some of the foraging strategies that lead to prey capture (ROPERT-COUDERT *et al.*, 2001). However, these techniques remain invasive, restricted to endothermic species feeding on ectothermic prey and are not easily applicable to large, aggressive individuals. Moreover, several limitations of the use of temperature recording for the estimation of the type and mass of ingested food have been noted (GALES and RENOUF, 1993; HEDD *et al.*, 1996; WILSON *et al.*, 1995a).

The measurement of jaw movement in free-ranging individuals has proved useful in providing information on the timing of prey intake of marine top-predators (PLÖTZ *et al.*, 2001; WILSON *et al.*, 2002), as well as grazing activity by herbivores (see review *in* BRUN *et al.*, 1984; COATES and PENNING, 2000). In addition, this approach is also reputed to deliver information about the type of prey ingested and, thus, allow allusion to diet composition. In these studies, loggers have been used to record the variation in an electromagnetic field between a sensor and a magnetic source. On free-ranging marine animals, magnets are attached to the animal's jaw with a sensor attached to the opposing mandible. When calibrated, the systems provide reliable estimates of prey size since variation in the electromagnetic field is dependent on the distance between the magnetic source and the sensor (WILSON *et al.*, 2002) and because animals swallowing larger prey whole tend to open their jaws wider and for longer. Proper calibration involves reconstruction of the opening angle of the subject's mouth in relation to the size of the ingested prey.

Although the utility of jaw movement detectors in assessing feeding activity of free-ranging penguins has been demonstrated (WILSON *et al.*, 2002) this method is potentially applicable to other animal species. In this study, we briefly consider the different types of feeding activity, principally herbivorous and carnivorous strategies that large vertebrates (turtles, seabirds, marine and terrestrial mammals) use in relation to quantities ingested over time. With the help of selected published or original examples we examine how jaw movement changes over time during ingestion.

II. MATERIAL AND METHODS

II.1. DATA LOGGERS

We used a jaw movement detector of the type described by WILSON *et al.* (2002) and LIEBSCH (2002). It consisted of a logger embedded in resin from which a 4-strand teflon cable (diameter 0.8-2.3 mm, length variable according to the investigated species) emerged and terminated in a Hall sensor (6 x 3 x 2 mm, KSY 10, Siemens GmbH, Siemens AG, Wittelsbacherplatz 2, 80333 Muenchen, Germany), the latter also being coated in resin (WILSON *et al.*, 2002). The Hall sensor was sensitive to changes in the strength of associated magnetic fields and reacted by producing a variable output which was stored in the memory of the logger. Two different types of logger, derived from the DKLOG 700 series (Driesen + Kern GmbH, Am Hasselt 25, 24576 Bad Bramstedt, Germany), were used during experiments: i) a one channel, 0.5-1.5 Mbytes Flash RAM, 133 x 19 x 25 mm, IMASEN (inter-mandibular angle sensor) logger (WILSON *et al.*, 2002), monitoring jaw movements only; and ii) a two channel, 10 bit resolution, round, 35 x 15 mm (25 g), IMASEN 2 logger (WILSON *et al.*, 2002), sampling depth and jaw movement data at the same frequency. The magnetic field was induced by square or round neodinium boron-rare earth magnets of various sizes (Table I) used solely or in pairs in order to increase the strength of the magnetic field.

II.2. SPECIES

In 2000–2002 we examined the utility of the jaw movement detectors to detect timing of prey ingestion and amount of food ingested, on 11 different species, from seven families (Table I). Most of the subjects were captive individuals, except for six, free-ranging Magellanic penguins, *Spheniscus magellanicus*, which were raising chicks at two different sites in Argentina (WILSON *et al.*, 2002). On captive and trained animals, the attachment and retrieval of loggers were performed by the keeper or trainer.

The attachment point and methods varied according to species (Figure 1). The attachment point of the logger on the body of the subject was primarily selected with regard to the aero- or hydrodynamic features of animals. For instance, in the case of marine animals the logger was placed at the point of the body where it created the lowest drag, *i.e.* caudally and on the center line of the back (BANNASCH *et al.*, 1994). Whenever possible, *i.e.* on species with fur or feathers, “tesa” tape (BDF, Beiersdorf AG, Hamburg, Germany) was the

TABLE I

Feeding type and name of species of the individuals *(n)* equipped with jaw movement detectors, and features of the experiments.

TABLEAU I

Comportement alimentaire et nom d'espèce (tortue à bec de faucon, manchot papou, manchot Adélie, manchot de Magellan, grand dauphin, otarie australienne, phoque veau-marin, chien domestique, sanglier, chèvre domestique et cheval domestique) des individus *(n)* équipés d'enregistreurs de mouvement de mâchoires, et caractéristiques des expérimentations (nombre, forme – cubique, circulaire, carrée – et taille des aimants ; lieu ; source).

Feeding types	Species *(n)*	Magnet number, shape and size	Location	References
Carnivores	Hawksbill turtle *Eretmochelys imbricata* (2)	2 cubic magnets (8x8x5 mm)	Museum of Marine Science, Stralsund, Germany	Liebsch, 2002
	Gentoo penguins *Pygoscelis papua* (3)	1 circular magnet (3x6 mm)	Nagoya Public Aquarium, Nagoya, Japan	Wilson *et al.,* 2002
	Adélie penguins *Pygoscelis adeliae* (7)	1 circular magnet (3x6 mm)	Nagoya Public Aquarium, Nagoya, Japan	Wilson *et al.,* 2002
	Magellanic penguins *Spheniscus magellanicus* (6)	1 square magnet (3x2x1 mm)	Cabo Virgenes & Isla Cormoran, Argentina	Wilson *et al.*, 2002
	Bottlenose dolphin *Tursiops truncatus* (1)	3 square magnets (27x8x2.5 mm)	Sea World Enterprises, Queensland, Australia	Ropert-Coudert *et al.,* 2002
	Australian sea lion *Neophoca cinerera* (1)	2 circular magnets (34x4.5 mm)	Sea World Enterprises, Queensland, Australia	Liebsch, 2002
	Harbour seal *Phoca vitulina* (1)	1 circular magnet (34x4.5 mm)	Seal Center, Friedrichskoog, Germany	Liebsch, 2002
	Domestic dog (1) *Canis familiaris*	1 square magnet (34x30x3 mm)	Lämmerstücken, Kiel, Germany	This paper
Omnivores	Japanese wild boar *Sus scrofa leucomystax*	1 circular magnet (34x4.5 mm)	National Agricultural Research Center for Western Region, Oda, Japan	Unpublished data
Herbivores	Domestic goat (1) *Capra hircus*	2 square magnets (34x30x3 mm)	Kiel, Germany	This paper
	Domestic horse (2) *Equus caballus*	2 circular magnets (34x4.5 mm)	Kiel, Germany	This paper

preferred method of attachment of the logger. This method reduced damage to the animals' feathers or fur (WILSON *et al.*, 1997). In the case of smooth surfaces, *e.g.* hawksbill turtle, *Eretmochelys imbricata*, or bottlenose dolphin, *Tursiops truncatus,* cyanoacrylate glue (Sekundenkleber, UHU GmbH & Co KG, Herrmannstrasse 7, 77815 Bühl, Germany) and suction cups, respectively, were used to attach the units.

Small sensors and magnets were attached directly face-to-face on opposing jaws. It was crucial to ensure that both the sensor and the magnet remained firmly in position throughout the experiment. Magnets were attached to the upper mandibles of gentoo penguins, *Pygoscelis papua*, the dolphin and the turtles, while they were placed on the lower jaw in Magellanic penguins, horses, a goat, dogs, a seal, and a sea lion. In the case of the hawksbill turtles, free-ranging penguins and bottlenose dolphins, magnets and sensors were glued to the side of the upper and lower jaws rather than placed dorsally and ventrally. This choice depends on the size of the subject species and the strength of the magnets. Clarity of the electromagnetic signals improved when the sensor was close to the magnets, *i.e.* ideally both should be placed on the edge of the "lips", at the rictus of the mouth. However, in large animals with flexible lips, such a method of attachment proved difficult. Better sites of attachment resulted in the magnets and sensors being placed further apart from each other necessitating the use of stronger, larger, magnets. In the case of the bottlenose dolphins, the Hall sensor and magnets were embedded in foam wrapped in cloth-backed "tesa" tape (Figure 1e) before being glued to the lower and upper jaw of the dolphin near the rictus. The logger was embedded in a hand-made silicon suction cup which was stuck on the left lower cheek below the dolphin's eye (ROPERT-COUDERT *et al.*, 2002a).

II.3. CALIBRATION OF THE LOGGER

Following the attachment of the logger and magnets, *in situ* calibrations of the system were performed on the Hall sensor output against the opening angle of the jaw. Although there was minor variation in protocol according to species, calibration consisted of inserting rods of increasing diameters (0.5–10 cm), one after the other, into the mouth of the subject at a known distance from the jaw articulation. Output values of Hall sensors (in millivolts) recorded by the loggers were regressed against jaw angle using standard equations (BARTH *et al.*, 1987). The best-fitting curves (all regressions used in the analyses had r^2 values greater than or equal to 0.99) were used to define jaw angle from the millivolt readings for data derived from feeding experiments (for details see WILSON *et al.*, 2002).

II.4. FEEDING EXPERIMENT PROTOCOL

All feeding experiments on captive animals were filmed using a digital video camera (GR-DVL 100, JVC Deutschland GmbH, Grüner Weg 12, 61169 Friedberg, Germany) recording 24 images per second, to further relate the jaw activity as determined on the video to the changes in voltage recorded by the data logger. Animals equipped with loggers were released in their usual

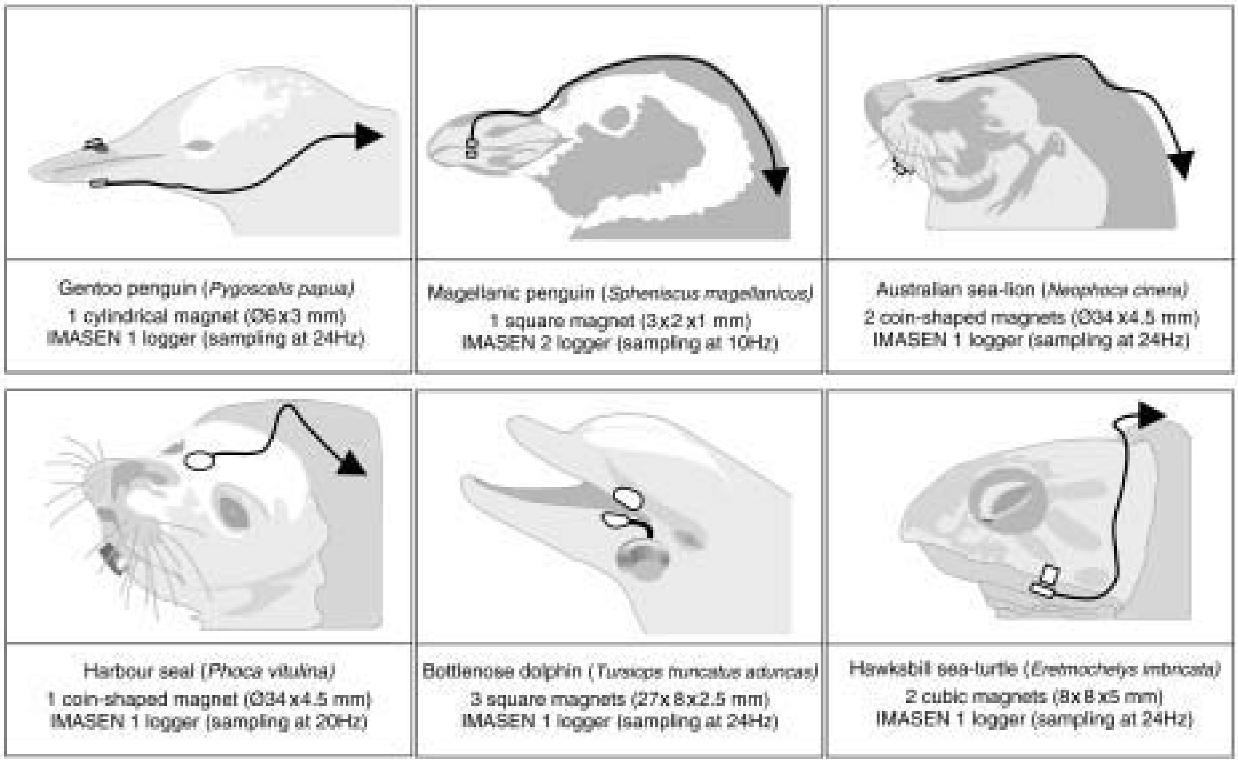

Figure 1: Description of the technology used to monitor the jaw movement, including the magnet shape and size, the type of jaw movement logger used and the position of attachment of the different elements illustrated on six species.

Figure 1 : Description de la technologie utilisée pour suivre les mouvements des mâchoires chez six espèces (manchot papou, manchot de Magellan, otarie d'Australie, phoque veau-marin, grand dauphin, tortue marine à bec de faucon) : forme (de gauche à droite et de haut en bas : cylindrique, carrée, en forme de pièce de monnaie, cubique) et taille des aimants, type et position d'attache de l'enregistreur et de ses éléments.

environment where they fed freely on various preys whose morphometrics were defined where possible. On occasion, however, the hosting institutes did not give us the time to determine prey morphometrics. Prey species were so chosen that they reflected the usual diet of the predator in its natural environment, for example: Antarctic krill, *Euphausia superba*, for Adélie penguins, *Pygoscelis adeliae.* Prey morphometrics were measured either with a ruler before they were fed to the animals, or by reconstructing the size of the prey from video footage. In some instances, prey body masses were measured to the nearest gram using a balance (PORTION POWER ™, Measurement Specialties Inc., 41 Plymouth St., Fairfield, New Jersey 07006, USA).

In assessing jaw angles to determine the ingested amount, we divided the ingestion process in four elements: (i) snap/pluck/mouth open to get the food initially past the extremes of the mouth apparatus; (ii) manipulation to get the food in the right position for (iii) and/or (iv); (iii) food mastication; and (iv) food moved back down to the throat.

II.5. ANALYSES

Simple regression (SOKAL and ROHLF, 1969) was used to test the relationship between prey morphometrics and the variables measured by the logger, *i.e.* duration and angle of mouth opening. All tests were performed using Statview (version 4.01, Abacus concepts, U.S.A. 1996). Values are presented as mean ± SD. For all tests, $P < 0.05$ was considered significant.

III. RESULTS AND DISCUSSION

III.1. LOGGER EFFECT

At the end of the feeding experiments, all parts of the equipment attached to the fur or feathers with TESA tape were easily removed. Glued parts, however, needed more care, sensors and magnets being cut loose from the fur or feathers with a scalpel or a special solvent. Whenever possible, the magnets were left on the animals at the end of the sessions until they came off one or two days later due to corrosion of the glue in salt water. The suction cup and all the items that had been glued to the skin of the bottlenose dolphin were easily removed at the end of the feeding session, indicating that they would not have remained in place for long and that improvement is needed before applying such systems on free-ranging cetaceans.

In every experiment, maximum care was taken to ensure that the animals were not exposed to unnecessary stress or harmful procedures. A reduced handling time is preferable since it tends to lead to a reduced rate of rejection of the logger by the animal (LE MAHO *et al.*, 1992). In this regard, the use of quick-drying glue, and TESA tape was very beneficial. For the experiments the delay between capture, equipment installation and release ranged from ca. 10 min (captive penguins) to ca. 75 min (hawksbill turtles). The logger was generally well-tolerated by the animals, with the horses, *Equus caballus*, goat, *Capra hircus*, turtles, sea lions, penguins and dolphins showing no apparent reaction to the device at all. The dog, *Canis familiaris*, made a few attempts to remove the unit before accepting it. Although the prey items given to captive individuals were similar to those captured in the wild, behavioral changes during capture and ingestion probably occurred. Captive animals may play with dead and live food items and many trained species are also accustomed to swallow dead items as a reward for their performance.

The opinions about the effect of applying a magnetic field close to the head of animals are controversial. Some studies show a disorientation of cetaceans to geomagnetic disturbance (BAUER *et al.*, 1985; KLINOWSKA, 1988) whereas other researchers are convinced that no interference exists (BRABYN and FREW, 1994; HUI, 1994). GUDMUNDSSON and SANDBERG (2000) suggest that the application of a strong magnetic field close to the head of animals may interfere with the animal's sense of navigation in species reported to use magnetic fields. Conversely, the behavior of penguins and turtles seems unaffected by the presence of a magnetic field close to their head (WILSON *et al.*, 2002; PAPI *et al.*, 2000). Similarly, a disorientation of harbour seals caused by the attachment of a magnet seems unlikely because these animals apparently orient themselves using auditory, visual or olfactory cues (JAMES and DYKES, 1977).

III.2. CONSIDERATION OF FOOD INGESTION BY VARIOUS ANIMAL CONSUMER TYPES

Figure 2 shows the expected curves of cumulative food ingested by carnivorous, herbivorous and drinking/lapping animals over time. These should not be confused with the three types of 'functional response' curves (HOLLING, 1959), for which the rate of prey consumption is dependent on prey density. Within the carnivorous group, a distinction can be made according to the size of the prey ingested. In the case of individuals that take a large prey from which pieces are bitten, *e.g.* lions or tigers, the consumption events are infrequent but during consumption the amount of ingested food is substantial and feeding may last several hours (Figure 2a). Carnivores that take large prey would feed often and it could be expected that small amounts of food be ingested over short periods (minutes), *e.g.* sea lions. Carnivores that capture small prey consume more frequently with small quantities of food that are quickly ingested, *i.e.* penguins ingesting krill items in seconds (Figure 2b). An exception in this scheme would be carnivores that swallow their large prey whole, *e.g.* some snakes (SECOR and DIAMOND, 1998). In contrast, herbivores such as deer or goats ingest food almost continuously at a slow but steady pace over several hours (Figure 2c). Mastication is necessary each time plants are taken which, therefore, is expected to produce small steps in the signals of cumulative mass of ingested food. Such small steps may be completely absent in the case of planktivorous animals that continuously and for hours (as long as the mouth remains open) may show a steady ingestion of particulate matter, *e.g.* whale sharks (Figure 2d). For animals that lap or drink, the food ingestion pattern is expected to be similar to that of herbivores, but this signal would occur in seconds or minutes only. The curve pattern of a lapping individual would show small steps in the cumulative mass of ingested food, whereas a sucking individual would be expected to approximate planktivourous animals.

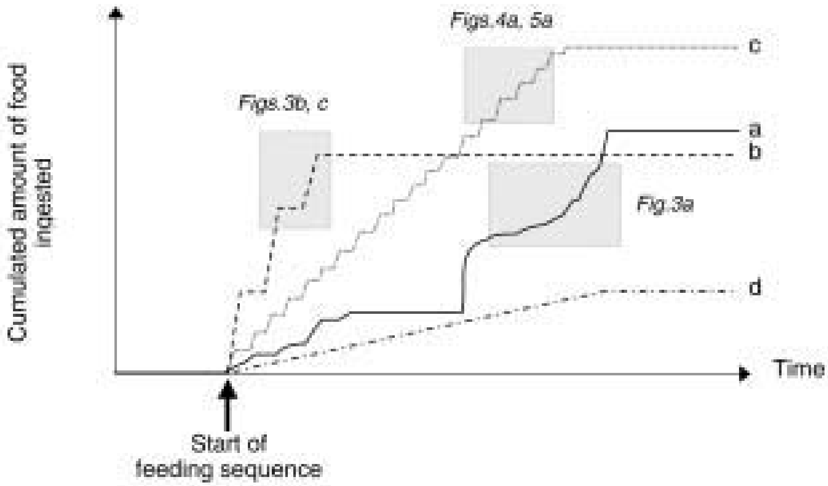

Figure 2: Expected signals (corresponding to cumulated amount of ingested food) delivered by a jaw movement logger in response to a feeding activity sequence by a) a carnivore eating large prey, b) a carnivore eating small prey, c) an herbivore grazing and d) an animal using a filter-feeding technique or drinking/lapping. The gray boxes send to Figures 3, 4 and 5 that present detailed signals for the cases a, b and c described in this figure.

Figure 2 : Enregistrements attendus (correspondant au cumul des proies ingérées) fournis par un enregistreur de mouvements des mâchoires manifestés au cours d'une séquence d'activité alimentaire par a) un carnivore mangeant de grandes proies, b) un carnivore mangeant de petites proies, c) un herbivore broutant et d) un animal utilisant une technique de filtrage des aliments ou buvant/lapant. Les fenêtres grises renvoient aux figures 3, 4 et 5 qui donnent le détail des enregistrements dans les cas a, b et c de cette figure.

III.3. DETERMINATION OF THE MASS AND TYPE OF INGESTED FOOD

For carnivores that are feeding on large prey, the substantial and frequent bites that serve to secure morsels of prey are apparent on the logger data, *e.g.* for dogs (Figure 3a). These bites are followed by apparent chewing and, sometimes less obviously, swallowing. As the size of the prey decreases, the number of bites required to capture it is generally likely to decrease to a single large snap being followed by mastication and swallowing, although this was not very apparent in our data from a captive Australian sea lion, *Neophoca cinerea,* ingesting live fish (Figure 3b). In marine animals, the ingestion of small prey did not involve mastication and the signal of swallowing directly followed an initial large grabbing peak, *e.g.* penguins swallowing sardines (Figure 3c). Squid ingestion by hawksbill turtles illustrates one variation of the carnivorous pattern. Here, vacuuming motions are apparent between the grabbing and chewing activity (Figure 3d) and the bill remains closed, holding the prey, while the buccal cavity expands creating a locally reduced internal pressure. When the beak is subsequently opened for a short period (Figure 3d), the prey is moved into the buccal cavity, sucked in by the pressure differential. In grazing herbivores it is difficult to count and discriminate between jaw movements associated with biting, manipulation and mastication (CHACON *et al.*, 1976).

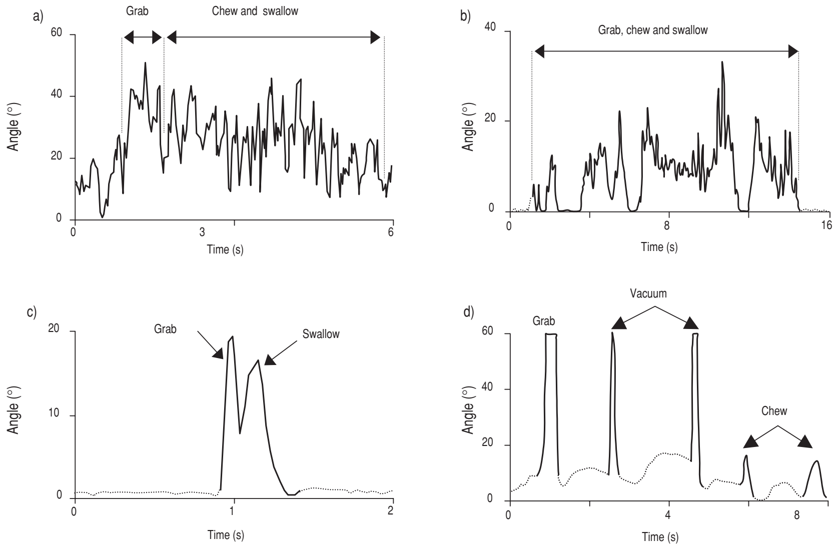

Figure 3: Fine temporal resolution of the signals (jaw angle in degrees) recorded by the jaw movement logger for four carnivorous individuals: a) dog, *Canis familiaris*, eating canned food, b) Australian sea-lion, *Neophoca cinerera*, eating live fish, c) Gentoo penguin, *Pygoscelis papua*, eating sardines, and d) Hawksbill turtle, *Eretmochelys imbricata*, eating squid, and resolution of the elements of the ingestion process.

Figure 3 : Description fine des signaux (angle des mâchoires en degrés) enregistrés au cours du temps par l'enregistreur de mouvement des mâchoires chez quatre individus carnivores: a) chien, *Canis familiaris*, mangeant de la nourriture en conserve, b) otarie australienne, *Neophoca cinerera*, mangeant du poisson vivant, c) manchot papou, *Pygoscelis papua*, mangeant des sardines, et d) tortue à bec de faucon, *Eretmochelys imbricata*, mangeant des calamars, et détermination des phases des processus d'ingestion (prise, mastication et ingurgitation chez le chien et l'otarie ; prise et ingurgitation chez le manchot ; prise, absorption à vide et mastication chez la tortue).

Automatic recording systems have been developed that can discriminate between grazing and other jaw movements (rumination, drinking, etc.) of sheep (PENNING *et al.*, 1984) and cattle (RUTTER *et al.*, 1997). In our study, plucking is apparent and can be distinguished from chewing via a modification of the frequency of oscillations in jaw angle (mean wave width at half peak height = 1.33 s , SD = 0.30, n = 35 for plucking events *vs* 0.62 s, SD = 0.11, n = 562 for chewing events, t = 31.9, $P < 0.001$ for a horse) but the jaw angle is very narrow, particularly in those species that are using their lips extensively to move matter into the buccal cavitiy, *e.g.* horses (Figure 4a). In this regard, a fast-Fourrier Transform analysis or the use of specific software that detects and quantifies bouts of jaw movements (RUTTER, 2000) may prove useful in differentiating between the various activities involved in grazing. Where animals open their mouth wider to feed, plucking may more readily be distinguished from chewing using the jaw angle, as well as via an assessment of chewing frequency (cf. Figures 4a and 4b). As for filter-feeding animals, the mouth is expected to remain wide open over a long period of time, which would result in an extensive jaw angle opening at a constant value in the data recorded by data loggers. Finally, recording jaw movements of a drinking dog showed that lapping activity could easily be detected. Lapping was detected as a high frequency oscillating pattern. Additional peaks were observed

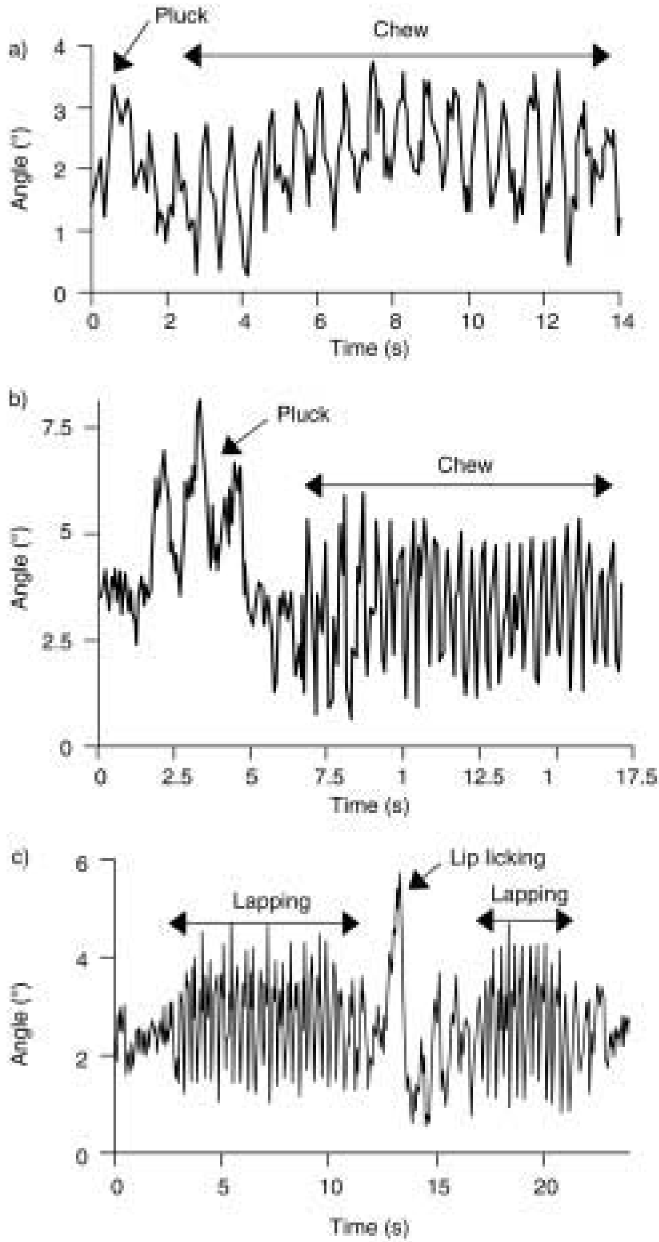

Figure 4: Fine temporal resolution of the signals (jaw angle in degrees) recorded by the jaw movement logger for two herbivorous individuals a) horse, *Equus caballus*, and b) goat, *Capra hircus*, and c) for a dog, *Canis familiaris*, and resolution of the elements of the ingestion process (plucking and chewing grass for the goat, lapping and drinking water for the dog).

Figure 4 : Description fine des signaux (angle des mâchoires en degrés) enregistrés au cours du temps par l'enregistreur de mouvement des mâchoires chez deux individus herbivores a) cheval, *Equus caballus*, et b) chèvre, *Capra hircus*, et c) chez un chien, *Canis familiaris*, et détermination des phases des processus d'ingestion (arrachage et mastication de l'herbe chez les herbivores ; lapement, léchage de babines et lapement chez le chien lapant et buvant de l'eau).

between lapping sessions. They corresponded to the dog licking its jaw with its tongue (Figure 4c).

Methods for estimation of food consumption must take account of the inter-specific variation in jaw angle associated with ingestion. However, some variables may intuitively appear more useful than others. The signal recorded by the logger may be related to the mass of the ingested prey via a single variable or a combination of variables. For example, the integral of the jaw angle over time and/or the duration of the event and/or mean maximum jaw angle and/or one, or multiple, counted jaw opening events may prove useful. For instance, the total duration of the jaw opening, as well as the maximum angle of jaw opening, appear to be related to the size of the ingested fish in harbour seals, *Phoca vitulina* (Figure 5a). On the other hand, the total number of peaks observed during ingestion events is a better predicator of the length of the squid's mantle in the case of hawksbill turtles (Figure 5b). In several instances, the integral under the curves of the peaks observed during ingestion events can be used to reliably estimate the mass of food ingested, *e.g.* in the case of a dog swallowing moist pre-processed food (Figure 5c) or in the case of penguins swallowing fish (WILSON *et al.*, 2002).

In addition to the mass, we speculate that the jaw movement recorder may help to determine the type of food ingested. WILSON *et al.* (2002) indicated that this might be the case in penguins, which are known to change prey in the wild (RIDOUX and OFFREDO, 1989; ROPERT-COUDERT *et al.*, 2002b). Ability to distinguish food types may be crucial in the case of omnivorous animals, such as wild boar, *Sus scrofa,* which feed on a variety of cultivated plants, roots, bulbs, and fruits (WOOD and ROARK, 1980; MASSEI *et al.*, 1996; BAUBET, 1998). Here, the determination of the food type may come from the use of an index derived from one or a number of various elements of the ingestion process. In this regard, sampling frequency is a key parameter to control, since this is critical in ingestion events (BOYD, 1993; WILSON *et al.*, 1995b; ROPERT-COUDERT and WILSON, 2004).

The rate at which food may be processed by the mouthparts may also be elucidated using jaw movement loggers. Qualitative analysis may be achieved by investigating the relationship of one the above-mentioned parameters with respect to another, *e.g.* the integral of the plucking peak divided by the number of consecutive chews in herbivourous individuals. We might expect that some food types require more chewing than others. Care must be taken here, though, because there likely will be considerable variability. An interesting example is where changes can be observed in the processing capabilities of a dog serially eating identical biscuits. In this example, both the duration of the ingestion and the total number of chews required to ingest the biscuits, serially decreased (Figure 6).

III.4. PROS AND CONS OF THE SYSTEM

Jaw movement recorders present both positive and negative aspects (Table II). Most of the negative aspects may be easily corrected since they depend on advances in technology: the development of smaller, less energy-spending electronic circuitry and increases in the memory of loggers. Technical progress may also improve the organization of field work, *e.g.* the use of a portable anesthesia system (GALES and MATTLIN, 1998) may facilitate work

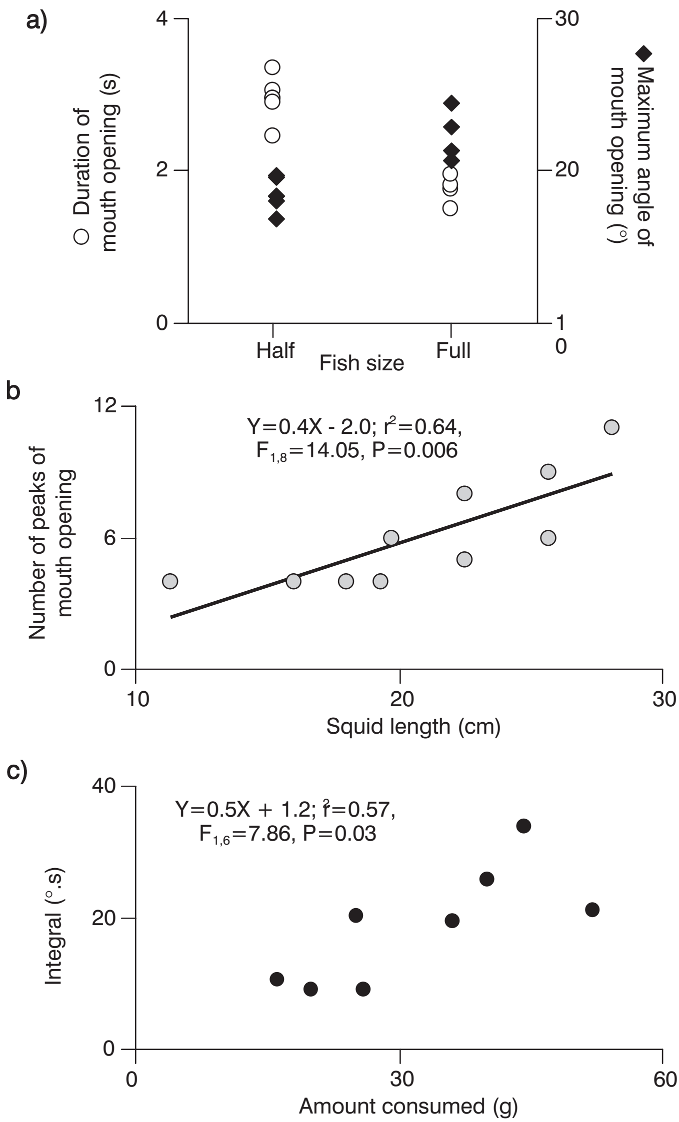

Figure 5: Quantitative assessment of the food ingested by animals using the signals recorded by the jaw movement loggers. In a) the duration and angle of mouth opening are negatively and positively related to the size of the fish ingested by a Harbor seal, *Phoca vitulina*. In b) the number of peaks of mouth opening by a hawksbill sea turtle, *Eretmochelys imbricata*, is linearly related to the length of the squid mantle. In c) the integral calculated under the curves of the peaks of mouth opening is linearly related to the mass of moist food ingested by a dog, *Canis familiaris.*

Figure 5 : Détermination de la quantité de nourriture ingérée grâce aux signaux enregistrés par les enregistreurs de mouvement des mâchoires. Le graphique a) montre que la durée (s) et l'angle maximum d'ouverture de la gueule (degrés) sont respectivement négativement et positivement liés à la taille du poisson ingéré par un phoque veau-marin, *Phoca vitulina.* Le graphique b) montre que le nombre de pics correspondant au nombre d'ouvertures du bec chez une tortue marine à bec de faucon, *Eretmochelys imbricata*, est relié linéairement à la taille du corps du calamar. Le graphique c) montre que l'intégrale calculée à partir des courbes de pics d'ouverture de la gueule est reliée linéairement à la masse de la nourriture fraîche ingérée par un chien, *Canis familiaris.*

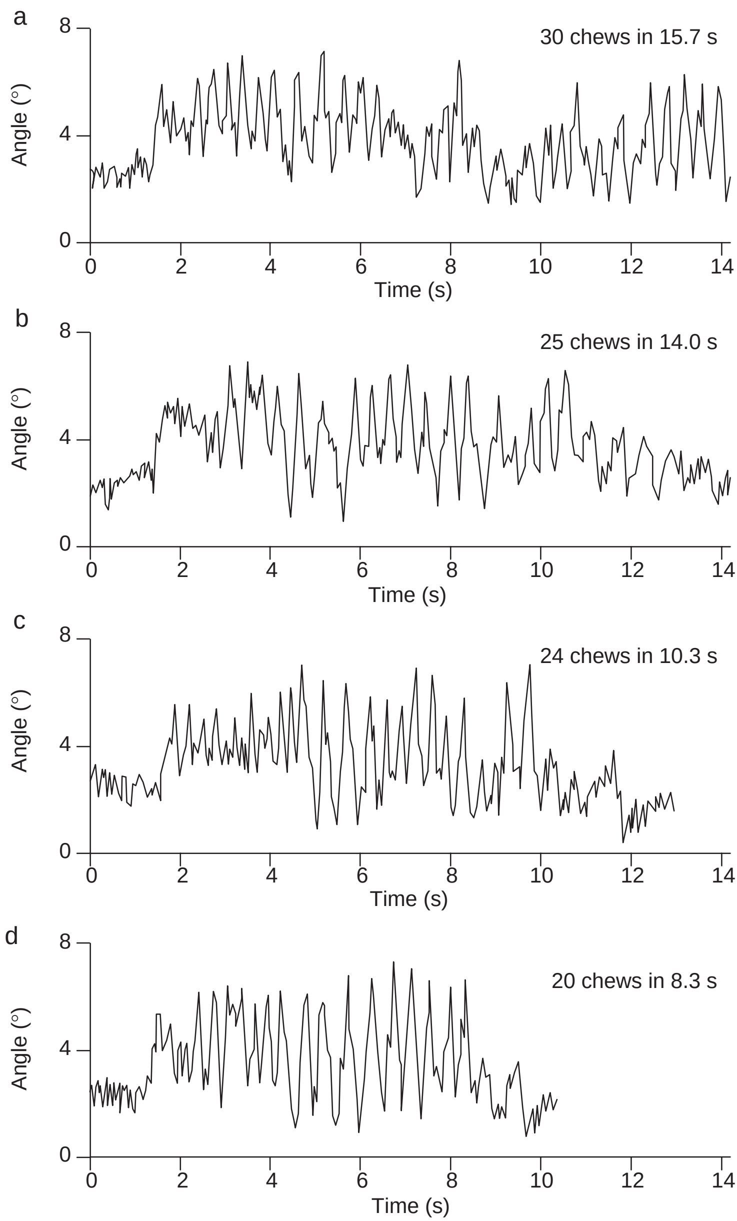

Figure 6: The type of food ingested by an animal might be qualitatively assessed using the signals (*e.g.* the chewing rhythm) recorded by the jaw movement logger, but changes in processing capabilities of a dog, *Canis familiaris*, serially eating identical biscuits, as presented here, suggest that care must be taken in such an assessment trial.

Figure 6 : Le type de nourriture ingérée par un animal pourrait être déterminé qualitativement par les signaux (par exemple le rythme de mastication) enregistrés par l'enregistreur de mouvement des mâchoires, mais les variations observées dans les processus d'ingestion au cours d'une série d'ingestions d'une même nourriture (des biscuits) par un chien, *Canis familiaris*, telles que présentées ici, suggèrent qu'il faut prendre des précautions quand on fait un tel essai de détermination.

on large-sized animals. However, aggression by conspecifics may be a serious difficulty when dealing with certain free-ranging species.

The loggers presented here provided interesting information on the timing of prey intake and the amount/quality of ingested prey. In comparison with other existing systems, *e.g.* recording of internal temperature, jaw movement data-loggers can be used in endothermic and exothermic predators seeking endothermic, exothermic, or both types of prey. Such an approach has also helped improve knowledge in grazing biomechanics and ecology (PENNING *et al.*, 1984; RUTTER *et al.*, 1997). The methodology may be suitable for free-ranging individuals, although it should be noted that recapture of terrestrial species for logger recovery may be more difficult than in marine species. In this regard, a transformation of the logger would be needed so that data could be transmitted rather than recorded. Another important feature is the consideration of the rate at which food matter passes into the mouth cavity and down the throat. For instances, some species use their tongue (penguins) or lips (horses) to pull or push the food back (a.k.a. the "conveyor-belt system"); some other jerk their heads to gulp (cormorants); or have specific suction systems (turtles). Researchers using jaw movement detectors should primarily identify whether the passage of food from the outside to the inside is punctuated or continuous. Equal care should be given to the behaviors associated with feeding although that may not be directly relevant to it, or to movements associated with vocalisations.

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TABLE II

Positive and negative aspects of the IMASEN (inter-mandibular angle sensor of jaw movement for vertebrates) logger methodology.

TABLEAU II

Aspects positifs et négatifs de la méthodologie utilisant l'enregistreur IMASEN pour l'enregistrement de l'angle inter-mandibulaire lors des mouvements des mâchoires chez les vertébrés.

Category *Sujet envisagé*	Positive aspects. *Aspects positifs*	Negative aspects. *Aspects négatifs*
Application *Mise en place*	1 - Non invasive. *Sans incision* 2 - Easily attached on fur and feathers *Facile à attacher sur fourrure ou plumage*	1 - May need anasthesia for free-ranging animals that are difficult to handle. *Peut nécessiter une anesthésie dans le cas d'animaux dans la nature peu faciles à capturer* 2 - Manipulation time depends on drying time of glue. *Le temps de manipulation dépend du temps de séchage de la colle* 3 - Conspecifics agonistic behaviour towards the logger or cable. *Comportement de peur vis-à-vis du détecteur ou du cable en fonction de l'espèce* 4 - Attachment difficult on individuals with flexible lips. *Difficultés d'attachement sur des individus aux lèvres flexibles*
Determination of the timing of prey intake *Détermination de la chronologie de prise de proies*	1 - Up to 100% detection. *Jusqu'à 100 % de détection* 2 - Distinction of elements of the ingestion process, *e.g.* grabbing, chewing, etc. *Reconnaissance des phases de l'ingestion : prise, mastication, etc.*	1 - Pre-calibration experiments are imperative. *Des expérimentations de pré-étalonnage sont impératives* 1 - Records of affailed capture and other activities, *e.g.* vocalization. *Enregistrement de prises alimentaires ratées et d'autres activités, par exemple des vocalisations*
Determination of the size of prey ingested *Détermination de la taille des proies ingérées*	1 - Potentially good (needs further calibration). *Potentiellement bonne (nécessite un étalonnage supplémentaire)*	1 - Difficult in carnivores feeding on large prey. *Difficile chez les carnivores ingérant de grandes proies* 2 - Difficult in the case of live prey (manipulation time) *Difficile dans le cas de proies vivantes (temps de manipulation)*
Other. *Autres*	1 - Can be used to monitor other behaviour (respiration, aggression, etc.). *Peut être utilisé pour suivre d'autres comportements (respiration, prédation, etc.)*	1 - Requires high sampling frequency and a large memory *Nécessite un rythme élevé d'échantillonnage et une grande mémoire*

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L'ENREGISTREMENT DES MOUVEMENTS DE MÂCHOIRES : UNE INDICATION DE L'ACTIVITÉ DE PRISE DE NOURRITURE

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MOTS-CLÉS: Carnivore, herbivore, mammifère, oiseau, tortue, enregistreur de données, mouvement des mâchoires, type d'aliment, ingestion.

RÉSUMÉ

Nous avons examiné si un enregistreur du mouvement des mâchoires, utilisant à la fois un aimant et un capteur de Hall placés en opposition dans chacune des deux mâchoires d'un même individu, était capable de fournir des indications sur l'activité d'ingestion des proies. Le capteur de Hall est un capteur sensible aux variations de champ magnétique engendrées par les mouvements des mâchoires. L'expérimentation a porté sur onze espèces animales de mammifères, d'oiseaux et de tortues en captivité, carnivores et herbivores exploitant des milieux terrestres ou marins. Après étalonnage du système, nous avons enregistré avec précision la chronologie de l'ingestion des proies dans tous les cas où la prise de nourriture avant son avalement a correspondu à une grande variabilité interspécifique de l'angle d'ouverture des mâchoires au cours du temps. Le pour et le contre concernant ce système est présenté ainsi que la possibilité de l'utiliser pour des études écologiques d'animaux dans la nature. Globalement ce système s'est révélé prometteur pour estimer la quantité et la qualité de la nourriture.

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