



SYMPOSIUM

Overview of FEED, the Feeding Experiments End-user Database

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Synopsis The Feeding Experiments End-user Database (FEED) is a research tool developed by the Mammalian Feeding Working Group at the National Evolutionary Synthesis Center that permits synthetic, evolutionary analyses of the physiology of mammalian feeding. The tasks of the Working Group are to compile physiologic data sets into a uniform digital format stored at a central source, develop a standardized terminology for describing and organizing the data, and carry out a set of novel analyses using FEED. FEED contains raw physiologic data linked to extensive metadata. It serves as an archive for a large number of existing data sets and a repository for future data sets. The metadata are stored as text and images that describe experimental protocols, research subjects, and anatomical information. The metadata incorporate controlled vocabularies to allow consistent use of the terms used to describe and organize the physiologic data. The planned analyses address long-standing questions concerning the phylogenetic distribution of phenotypes involving muscle anatomy and feeding physiology among mammals, the presence and nature of motor pattern conservation in the mammalian feeding muscles, and the extent to which suckling constrains the evolution of feeding behavior in adult mammals. We expect FEED to be a growing digital archive that will facilitate new research into understanding the evolution of feeding anatomy.

Introduction

Much of our understanding of the evolution of mammalian craniofacial form and function relies on physiologic studies of the motor patterns, movements, and forces generated during feeding (Hiimeae 1976, 1978, 2000; Crompton and Hylander 1986; Herring 1992; Weijs 1994; German and Crompton 2000; Hylander et al. 2004; Crompton et al. 2007). These studies provide insights into the function of a suite of unique anatomical synapomorphies involved in mastication, suckling and swallowing (Crompton et al. 1978; Crompton 1989; Smith 1992) as well as other dietary adaptations that were critical during the origin and subsequent diversification of

mammals (Crompton 1963, 1989; Turnbull 1970; Hiimeae 2000;). Mastication, suckling and swallowing in mammals are coordinated by the tongue, palate, hyoid, as well as neomorphic groups of facial and pharyngeal elevator and constrictor muscles. Together, these derived morphological and behavioral features suggest that mastication, suckling and swallowing in mammals are unique behaviors (Smith 1992). While these traits define mammals, the appearance of many of them at the origin of the Class represented a significant opportunity for diversification and subsequent evolution of the mammalian feeding apparatus (Crompton et al. 1978).

The physiology of mammalian feeding is documented extensively in large amounts of *in vivo* data collected over the past 40 years. However, our ability to undertake comparative studies that effectively synthesize these data is limited by the enormous task of compiling the datasets into uniform digital formats and making them broadly accessible for analysis. Additionally, the lack of a standardized terminology for describing and organizing these data from multiple sources makes their joint interpretation difficult. In order to address this gap, an international group of mammalian feeding physiology researchers formed the Mammalian Feeding Working Group. In collaboration with the National Evolutionary Synthesis Center (NESCent), the objective of the Working Group is to develop the informatics infrastructure and the intellectual framework for enabling multi-species studies of mammalian feeding physiology.

The first goal of the Working Group is to develop the infrastructure necessary for generating a comprehensive, multi-species digital repository of data on mammalian feeding physiology, called the Feeding Experiments End-user Database (FEED). *In vivo* physiologic data are difficult to manage and manipulate because of their inherent complexity, particularly with regard to interpreting the data within the context of the experimental design and to linking the data to behaviors and morphology. These characteristics motivate the development of standards for the incorporation of supporting metadata to make the data usable by a broader scientific community.

The second goal is to compile the data housed at different research laboratories and stored on different types of media into FEED. Creating a comprehensive database for mammalian feeding data is timely for a variety of reasons. Most important among these are (1) meeting the expectations of the biological community to promote public access to data for continued use in research and education, (2) providing a centralized archive for existing datasets and a repository for new data sets, (3) reducing the unnecessary duplication of data obtained *in vivo*, and (4) facilitating integration of data in analyses that extend across disciplines (Russell and Burch 1959; Halaynch and Goertzen 2009; Whitlock 2011). FEED also provides a model for other comparative physiologists and functional morphologists interested in developing multi-species databases of physiologic data.

The third goal is to use the data in FEED to conduct a number of comparative analyses aimed at exploring synthetic questions concerning mammalian feeding. Quantitative analyses of this scope require a database designed to permit consistent use of the raw

physiologic data. These studies are a critical next step in research on mammalian feeding because they will help us connect variation in feeding physiology to broad-scale patterns of mammalian evolution and diversification (Hiimae 2000).

In this article, we review the species representation, the physiologic data, and the supporting metadata in the first public release of FEED. We present the scientific rationale behind the data model for FEED and outline the controlled vocabulary that provides the basis for consistent use of the physiologic data in scientific analyses. The subsequent papers in the symposium begin work toward the goal of synthetic analyses of mammalian feeding. The breadth of these papers as a group, and the depth of individual papers addressing fundamental questions, illustrate the tremendous potential that FEED holds for future studies of feeding in mammals.

Overview

FEED is populated with physiologic data and metadata from research on mammalian feeding. The public version of FEED can be accessed online directly at www.feedexp.org by following the links provided on the website.

Species composition

The public version of FEED contains physiologic data for 16 mammalian species in nine orders (Supplementary Table 1). The species composition includes animals that consume a variety of diets, and that vary in molar occlusal pattern, and oropharyngeal and craniofacial morphologies. Several of the species have been used as *in vivo* research models for studying feeding physiology over the past several decades (e.g., *Sus scrofa*, *Oryctolagus cuniculus*, *Macaca fascicularis*). In addition to data on adults, there are several types of physiologic data for infant and juvenile individuals of *Sus scrofa* and *Oryctolagus cuniculus*.

Over the next several years, we plan to add datasets to FEED through digital conversion of data archived on analog storage media and through accession of digital datasets currently being collected by members of the Working Group (Supplementary Table 1). The archived data are a priority as they include many of the seminal studies on mammalian feeding that were conducted on difficult-to-acquire species (e.g., tenrecs, some primates). Some of these species occupy key positions on the mammalian phylogeny and demonstrate morphological and behavioral transitions as well as derived states (e.g., Oron and Crompton 1985). Moreover, many

Table 1 Types of physiologic data in FEED

Type of data	Physiologic information	Potential interpretations
Electromyography	Motor unit activation	Timing and magnitude of muscle activity
Sonomicrometry	Muscle Strain ($\Delta L/L$)	Type of muscle contraction
Strain Gages	Bone Strain ($\Delta L/L$)	Patterns of bone deformation
Force & Pressure Transducer	Reaction Forces	Bite forces & oral pressures
Kinematics	Tissue Movements	Result of muscle activity

of these data are stored on analog media that has the potential to degrade and for which it is becoming increasingly difficult to find the equipment necessary for analog-to-digital conversion (e.g., magnetic tapes). These “legacy data” substantially increase the phylogenetic breadth of FEED and add to the types of physiologic data available for analysis.

Physiologic data

The physiologic data in FEED are recorded using a variety of sensors. The bulk of the data are electromyographic (EMG) recordings of activity patterns in the craniofacial and oropharyngeal muscles during feeding. EMG is a technique that records the action potentials in muscles during recruitment (Basmajian and De Luca 1985; Loeb and Gans 1986) and provides data on the timing, amount, and duration of activity (Table 1). FEED also includes a significant amount of *in vivo* data for other aspects of feeding such as sonomicrometric recordings of muscle strains (Konow et al. 2010), strain gage recordings of bone strains, transducer measurements of bite forces along the dentition, measurements of oral pressure during feeding or suckling, and kinematic data on various tissue movements (Table 1). In many cases, data from two or more types of sensors are collected simultaneously, allowing researchers to use data in FEED to analyze (1) how muscles generate force and movement during feeding, (2) the ways in which forces are resisted by the skull, and (3) the functional outcomes of the forces and pressures generated during feeding.

Metadata

The metadata are essentially a digital laboratory notebook to store information and illustrations about the equipment, such as sensors, and protocols used to acquire data, the research subjects, and the anatomical structures from which the sensors recorded information. The metadata provide the information required to interpret the data, including sampling rates, types of sensors, and channel lineup. They incorporate comprehensive controlled

vocabularies pertaining to sensors, species, protocols, anatomy, the developmental stage of the research subject, and feeding behaviors. Not all metadata fields are required for the deposition of physiologic data into FEED. However, each entry requires key aspects of the metadata including such attributes as species name, digital recording rate, and channel lineup.

Controlled vocabularies

An important function of the controlled vocabularies is to facilitate combining the individual datasets into a coherent database that permits synthetic analyses and long-term use of the data by non-Working Group members. The vocabularies and their associated definitions are a necessary first step towards generating several orthogonal ontologies for use in conjunction with FEED.

The controlled vocabulary for data-acquisition protocols contains primarily technical, positional, and measurement terms (Supplementary Table 2). Another vocabulary standardizes how the developmental stage of a research subject is classified (Supplementary Table 3). Developmental stage is related to many physiologic and morphologic parameters (including dental eruption state, muscle anatomy, bone material properties, and sutural fusion) and is thus an important variable.

Finally, there is a controlled vocabulary of anatomical structures and locations comprising 43 muscles or muscle divisions and nine bones or regions of the head (Supplementary Table 4). This list incorporates all of the muscles of the craniofacial and oropharyngeal regions that are known to be involved in mammalian feeding. Morphology is central to meaningful interpretation of the physiologic data in FEED. Anatomical names should ideally convey evolutionary meaning by describing homologous structures across the taxa of interest. Within mammals, there is compelling positional, innervation, and embryologic evidence that the muscles we include in our terminology are homologous at the level of the whole muscle. However, there is much less consensus as to how to determine and name the anatomical divisions

Table 2 Controlled vocabulary and definitions for feeding behaviors

Bite	Bite force production while grasping a substance with the jaws.
Isometric Bite	Bite force production with no motion of the jaws.
Ingestion	Initial acquisition and movement of a food or liquid substance from outside to inside the body.
Mastication	Food breakdown using the postcanine dentition ^a .
Intraoral food processing	Food breakdown by structure(s) of the oral cavity (e.g., palatal rugae).
Intraoral transport	Movement of food or liquid from the lips through the oral cavity and into the pharynx. For food, this can include Stage I and Stage II (Hiimae 2000).
Swallow(ing)	Movement of food or liquid through the pharynx and into the esophagus.
Complete feeding sequence	Movement of a substance from outside the body into the esophagus, and containing all processes/events: biting, ingestion, intraoral transport, mastication, swallowing, and oral food processing.
Feeding sequence	A sub-set of processes/events during movement of a substance from outside the body into the esophagus, including some of the following: biting, ingestion, intraoral transport, mastication, swallowing, and oral food processing.
Complete drinking sequence	Movement of fluid from outside the body through the pharynx and into the esophagus containing all processes/events: ingestion, intraoral transport, swallowing.
Drinking sequence	Movement of fluid from outside the body through the pharynx and into the esophagus, including some of the following: ingestion, intraoral transport, swallowing.
Suckle	Negative or reduced pressure in the oral cavity that gets fluid out of a nipple and into the oral cavity.

^aThere was intense discussion by the Working Group about whether to include a number of features of mastication that characterize most mammals. These features are precise occlusion of the postcanine dentition, unilateral placement of a food bolus, and transverse motion of the lower jaw during the power stroke. In the end, the decision was made to define mastication without reference to these commonly occurring mammalian characteristics in order to ensure that the initial analyses using FEED, based on search and download using mastication as a search term, include as many datasets as possible.

(parts) within some of these muscles (e.g., the parts of the masseter muscle) and whether such parts are homologous across Mammalia.

The physiologic data encompass a total of twelve feeding behaviors, all of which have been strictly defined by the Working Group. The definitions (Table 2) are considered operational definitions and working hypotheses relevant to studies of the evolution of mammalian feeding, and more generally, vertebrate feeding.

Contributing to and using FEED data

FEED is designed to permit quantitative, phylogenetically-informed analyses of physiologic data. Therefore, contributions should include complete feeding and drinking sequences whenever possible. However, incomplete feeding sequences on species that are rare and difficult to acquire, species that exhibit unusual feeding morphologies, or species that increase the phylogenetic representation in FEED are also important. The metadata fields designated as “required” aim to provide sufficient information adequate for users to reconstruct the physiological state of the research subject at the time of data collection and to determine whether the raw data are applicable to a specific research question. Beyond these minimum requirements,

contributors are encouraged to annotate their data as thoroughly as possible with text boxes and relevant illustrations of waveform graphs, equipment, and morphology. More detailed guidelines are provided in Supplementary Table 5. Publications using or including data sets downloaded from FEED should cite both the original data collector(s) and FEED. In addition, FEED allows users to request to be connected directly to the original collector(s) of a chosen dataset. For general guidelines on data reuse and attribution see Whitlock (2011).

Data model

The data model of FEED unifies the representation and format of physiologic data on mammalian feeding across a range of sensor technologies, diets, behaviors, and species. It was designed using the combined domain expertise of the Working Group, with the goal to facilitate quantitative comparative analysis and to be useful as a scientific tool for researchers in such disciplines as bioengineering, evolutionary developmental biology, systematics, and ecology.

FEED consists of the recordings of raw physiologic data and the metadata, which describe the subject and acquisition of the data, and organize the data records into related experiments and studies.

The raw physiologic data are stored in tab-delimited text files, with each column holding a stream of (floating point) numbers coming from an equipment channel. Each such stream represents the waveform values recorded from a structure during feeding using some type of sensor (e.g., indwelling EMG electrode). The waveform values are “raw” in that they have not been manipulated (e.g., smoothed, rectified, or integrated) beyond the initial amplification and/or filtering that occurred at the time of data collection. In addition, channels can be included for carrying time stamps or behavioral events synchronized with the waveform values.

The metadata are arranged hierarchically (Fig. 1). A Study serves as a top-level data container and typically includes data collected for several animal or human subjects. Each Experiment within a Study is a single implantation of a set of sensors in one research subject. An Experiment may employ multiple techniques for data collection (e.g., EMG and bone strain) and may contain several Recording Sessions. Each Recording Session corresponds to a single hook-up of sensors to recording equipment. Trials appear sequentially within a Recording Session, and each Trial is associated with one tab-delimited file of raw physiologic data.

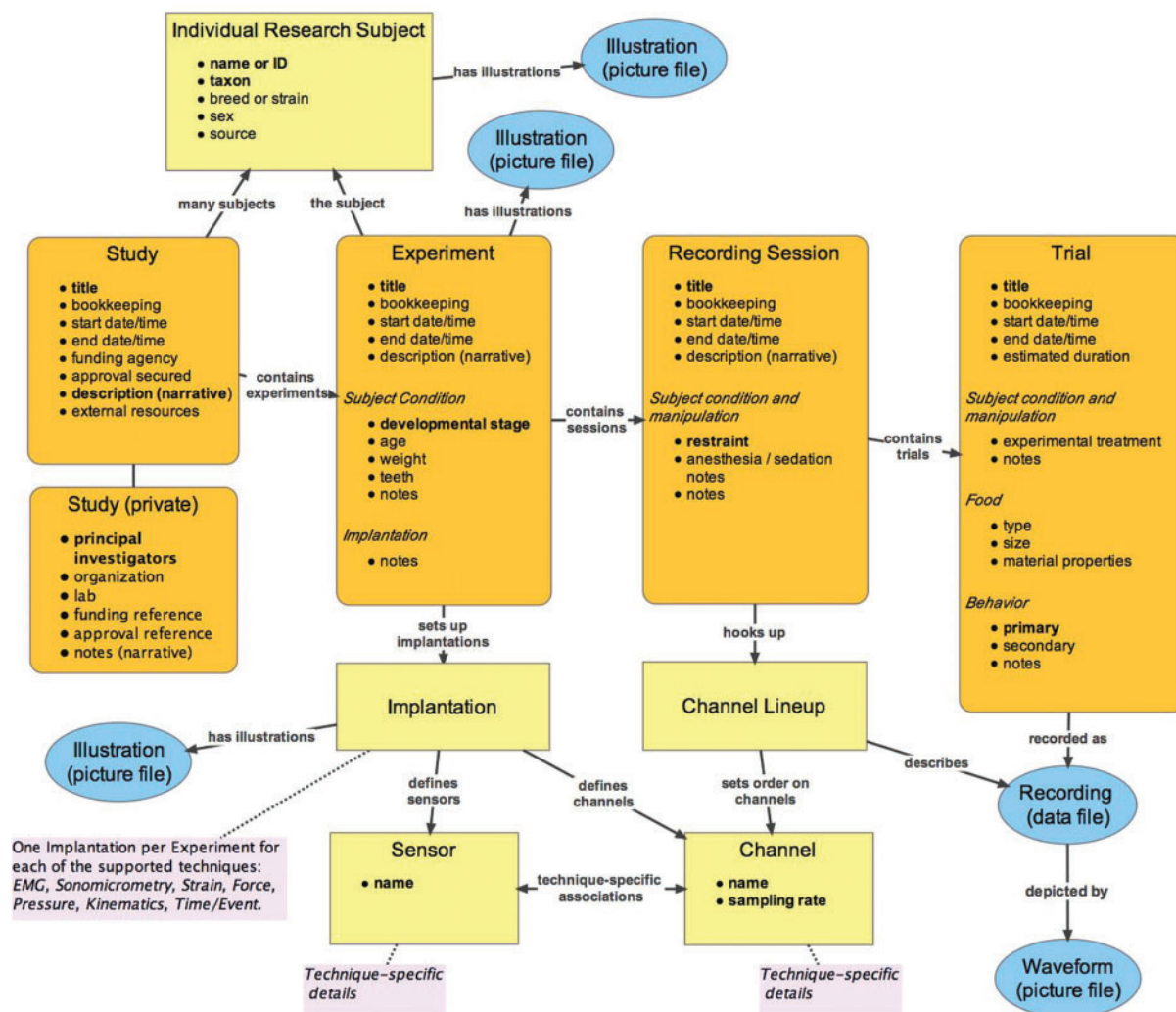


Fig.1 The data model. The orange rounded rectangles denote the containers for the hierarchical organization of metadata associated with the physiologic data. The Study container is divided into public and private portions. The yellow angular rectangles denote the types of metadata that are arranged within each container. A partial list of the types of metadata attributes is provided for Study, Experiment, Recording Session, Individual Research Subject, Sensor, and Channel. The blue ellipses denote files stored in the system, which can be either the raw physiologic data recordings collected during a trial or illustrations associated with particular aspects of the metadata. The light purple rectangles comment on technique-specific aspects of the data model that are not represented in the diagram explicitly.

In addition, metadata records identifying Subjects and their taxonomic information are linked to Studies and Experiments. Each data container allows for the upload of illustrations and the addition of unstructured textual descriptions. Further description of the data containers is provided in Supplementary Data 1.

The data standards that promote broad reusability of the physiologic data are the adoption of the hierarchical arrangement of the data containers where a trial is the individual unit of analysis, and the archiving of raw data, rather than smoothed and/or integrated data. The hierarchical design derives from the nature of experimental data collection and minimizes redundancy between the metadata records. The use of raw data allows greater flexibility in downstream analysis of waveform data. This is important since it is not possible to anticipate all future uses of the physiologic data, many of which might require data that have not been smoothed or integrated. The nesting of Sensor implantation and hook-up under Experiment and Recording Session, respectively, is an important innovation of FEED that creates a common framework for accurately storing information about the variety of technique-specific experimental setups.

The use cases

The Working Group developed a set of five collaborative research projects, or *use cases*, that aim to provide the context for future work on the evolution of mammalian feeding physiology using FEED. The use cases focus on providing a phylogenetically informed examination of the links among behavior, function, and morphology. Many of the papers in this issue of *Integrative and Comparative Biology* comprise initial analyses within the use cases.

Use Case 1: Investigations of Homology of Mammalian Feeding Muscles. Numerous studies have documented the anatomy of the mammalian oropharyngeal muscles (e.g., Edgeworth 1935; Schumacher 1961; Hiimae and Jenkins 1969; Turnbull 1970; Smith 1992, 1994; Mu and Sanders 1998; Druzinsky 2010a, 2010b; Perry et al., submitted for publication). The paper by Druzinsky et al. 2011 is a first step in describing variation in the jaw adductor musculature among mammals using up-to-date molecular phylogenies and modern phylogenetic comparative methods. In the future, this work will be expanded to consider biological homology (Wagner 1989; Smith 1994) and functional similarity of the feeding muscles across a broader range of mammalian species.

Use Case 2: Character Evolution in Mammalian Feeding Physiology. A central question we will ask using the data in FEED is “when and how did key physiological variables for feeding evolve across mammals?”. Data for all available species will be placed on a mammalian phylogeny to highlight major changes in character state throughout mammalian evolution. This will present a synthetic analysis of character evolution for variables in feeding physiology across mammals (see Williams et al. 2011; Vinyard et al. 2011).

Use Case 3: Evolution of the Development of Motor Pattern in Mammals. The name Mammalia refers to the presence of mammary glands, and suckling is a mammalian synapomorphy. Yet, almost no work exists on the evolution of suckling across mammals or the evolution of the transition from suckling to eating solid food (German and Crompton 2000; Thexton et al. 2008). The overarching questions for this use case are: (1) Is the motor pattern underlying suckling a synapomorphy of mammals and (2) do subsequent ontogenetic changes from an infant to an adult feeding pattern reflect specific adaptations to diet and behavior that characterize different taxa of mammals?

Use Case 4: Conservation of Motor Pattern in Mammals. No consensus exists on the conservation of motor pattern, and much of the debate focuses on feeding muscles (Hiimae 1978; 2000; Bramble and Wake 1985; Smith 1992, 1994; Weijs 1994; Alfaro and Herrel 2001; Alfaro et al. 2001; Herrel et al. 2001, 2008; Wainwright 2002; Williams et al. 2007; Wainwright et al. 2008). Conservation of motor pattern appears to be characteristic of some vertebrate groups (Wainwright 2002), but has not been examined rigorously in mammals. Qualitative assessments of motor pattern in mammals are based on the activity patterns of the jaw adductors and indicate diversification of motor pattern during mammalian evolution (e.g., Weijs 1994). We will examine hypotheses contrasting conservation (i.e., homology) and convergence of motor pattern within the context of the potential for significant modulation of feeding motor patterns in mammals (Smith 1992). These analyses will re-focus the debate on the mechanisms controlling the movement of food through the mouth and pharynx rather than on mastication as an isolated behavior and will evaluate whether the coordination between jaw and tongue movement during mastication and transport is conserved in mammals such that the sequence of activity of the muscles is maintained with minor changes to duration and intensity (A. Crompton, personal communication).

Use Case 5: Patterns of Coordination of Jaw-Muscle Activity in Herbivorous Mammals. Coordination among muscles is required to perform specific tasks requiring complex movements. Because at least eight muscles or muscle compartments produce complex jaw movements during the closing phase of chewing (i.e., fast-closing and the power stroke), the feeding system of mammals provides an ideal model for testing evolutionary changes in patterns of muscle coordination for producing similar movements or behaviors (Hiimae and Crompton 1985; Hiimae 2000). Herbivorous mammals, in particular, exhibit large changes in the direction of jaw movements during chewing yet precise coordination facilitates a smooth transition as the jaw is redirected (e.g., De Vree and Gans 1976). The multiple, independent evolutionary origins of herbivory across mammals provide a worthwhile test case for studying convergence in muscle coordination related to function and diet (see Crompton 2011; Williams et al. 2011).

Discussion and conclusions

With FEED, we initiate the process of making physiologic data publically available for scientific analyses. This availability is critical for enhancing our ability to characterize the significant features of mammalian feeding physiology and for generating hypotheses explaining the factors and events underlying the evolution of the mammalian feeding apparatus. The creation of multi-species databases for other vertebrate groups, many of which are better sampled in terms of species number, would allow scientists to broaden the scope of analyses of feeding to include fish, amphibians, and reptiles (Wainwright et al. 2007). It is our hope that FEED is a step toward making available the physiologic data necessary for systems biology research (Phillipi and Köhler 2006).

FEED is designed to enable hypothesis-driven, synthetic and cross-species analyses. The subsequent papers in this issue put the data in FEED to work by beginning the tasks of making broad phylogenetic comparisons of feeding traits (Crompton 2011; Druzinsky et al. 2011; Konow et al. 2011; Vinyard et al. 2011; Williams et al. 2011); understanding the connections between the ontogeny of suckling and feeding and the physiology of the adult feeding apparatus (Campbell-Malone et al. 2011; Langenbach 2011); and refining biomechanical and evolutionary hypotheses to better explain the functional significance of morphological features in the feeding apparatus (Herring et al. 2011; Iriarte-Díaz et al. 2011; Terhune et al. 2011). These studies are characterized

by the use of hypothesis-driven approaches and the goal of offering a synthetic interpretation of the meaning of their results for mammalian evolution. Over the next two years, in addition to our work in populating FEED with legacy and current data from Working Group members, we will proceed with extending the analyses presented in this issue as we continue to explore these use cases and other synthetic questions related to mammalian feeding.

The public version of FEED is available at www.feedexp.org. Through 2012 and 2013 we will continue to improve the design of FEED and to add both legacy and newly collected datasets. By the end of 2013, the aim is to have populated FEED with data from 11 orders and 47 species (Supplementary Table 1). Data release to the public is gradual because uploading raw physiologic data and entering high-quality metadata is a very labor-intensive process that Working Group members are doing on their own time. However, as many funding agencies and scientific journals in evolutionary biology (e.g., *Journal of Evolutionary Biology*, *Evolution*, and *The American Naturalist*) are imposing data archiving and sharing requirements (Moore et al., 2010; Rausher et al., 2010; Whitlock et al., 2010), we have developed FEED with the intent of ultimately becoming a repository for other researchers to store their physiologic data on feeding and release it to the public.

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Supplementary Data

Supplementary Data are available at *ICB* online.

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