New Insights into the Physiology of Natural Foraging*

Jennifer M. Burns[1]
Terrie M. Williams[2]
Stephen M. Secor[3]
Norman Owen-Smith[4]
Naomi A. Bargmann[1]
Michael A. Castellini[5]

[1]Department of Biological Sciences, 3211 Providence Drive, University of Alaska, Anchorage, Alaska 99508; [2]Department of Ecology and Evolutionary Biology, 100 Shaffer Road, University of California, Santa Cruz, California 95060; [3]Department of Biological Sciences, University of Alabama, Tuscaloosa, Alabama 35487; [4]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits 2050, South Africa; [5]Institute of Marine Science, University of Alaska, Fairbanks, Alaska 99775

ABSTRACT

The purpose of this symposium was to examine how foraging physiology is studied in the field across a diversity of species and habitats. While field studies are constrained by the relatively poor ability to control the experiment, the natural variability in both the environment and animal behavior provides insights into adaptation to change that are usually not tested in the laboratory. Talks in this session examined how foraging energy (both costs and gains) is partitioned over time. "Time," in this case, ranged from evolutionary time (how different animals are designed to most efficiently forage), to long, lifetime periods (development of foraging ability and growth), to short-duration feeding bouts, and ultimately to the minutes to hours following ingestion (metabolic and biochemical changes). From this diversity, two core themes emerged: that foraging strategies and behaviors are limited by physiology and biochemical processes and that time plays a central role in the organization of foraging behaviors and the physiological processes that underlie those behaviors.

Introduction

The purpose of this symposium was to examine how foraging physiology is studied in the field. Our goal was to provide an overview of how a diverse group of researchers approached the study of foraging ecology in birds, mammals, and reptiles. Because the physiological processes involved in foraging range from behavioral adaptations to molecular mechanisms, talks in this session covered a variety of topics. While such an approach precludes the a priori identification of a single unifying theme, we were interested in understanding whether the natural variability in both the environment and animal behavior could provide insight into patterns of adaptation or behavior not evident in laboratory studies. Therefore, symposium speakers focused on using field data to test hypotheses about how behavioral strategies and environmental conditions influence foraging and digestive efficiency, developmental patterns and growth rates, and the applicability of new biochemical tracers of digestion. From this diversity, two core themes emerged: that foraging strategies and behaviors are limited by physiology and biochemical processes and that time plays a central role in the organization of foraging behaviors and the physiological processes that underlie those behaviors. What follows is a brief review of symposium presentations and the conclusions that we drew from the resulting discussions.

Using Time: The Efficiency of Different Foraging Strategies

A general metric for success by an animal or animal population is the balance between energetic costs and benefits (Stephens and Krebs 1986). For terrestrial predators, achieving this balance involves a wide range of behaviors and hunting techniques that vary in duration, locomotor costs, and energetic reward (see, e.g., Schaller 1972; Packer et al. 1990; Estes 1991; Caro 1994). Because foraging occurs underwater for most species of marine mammal, less is known about the specific hunting behaviors or energetic costs of foraging in these predators (Williams and Yeates 2004). The few available studies indicate that this group, like terrestrial predators, uses a variety of behavioral techniques to capture prey, including high-speed pursuits of large prey items (Davis et al. 1999) and slow skimming through swarms of tiny krill, as observed for mysticete whales (Acevedo-Gutiérrez et al. 2002). For both marine and terrestrial predators, numerous small prey or single large prey items may be taken to satisfy daily energy needs. In addition, cooperative hunting (e.g., Gorman et al. 1998; Baird and Whitehead 2000) and solitary forays (e.g., Caro 1994; Davis et al. 1999) may occur in terrestrial and aquatic habitats, depending on the species and particular prey.

Marine mammal predators are also constrained by physiological and physical factors that are unique to hunting in water (Dejours 1987). The most important of these is access to air, which limits the duration of individual foraging dives. In view of this, the temporal pattern of energy acquisition will likely differ between marine and terrestrial carnivores. To examine how hunting methods and habitat type influence the energetic costs and benefits of foraging in carnivores, Williams and Yeates (2004) determined the energetic cost of hunting dives, energy acquired from ingested prey, and patterns of energy acquisition in two marine mammals, the Weddell seal (*Leptonychotes weddellii*) and the sea otter (*Enhydra lutris*), and compared results with those published for foraging activities of two terrestrial predators, the African wild dog (*Lycaon pictus*) and the African lion (*Panthera leo*).

When examined at the level of a single hunting event (either a foraging dive or the time required to capture a single prey item), the hunting efficiencies of marine and terrestrial animals differ markedly. As might be expected, the duration of individual hunting forays was significantly lower for the two marine mammal species examined than for the terrestrial species. However, the marine mammals spent a greater percentage of the day hunting than the terrestrial mammals. Energy gained per energy expended per hunting event for the marine mammals was equal to or higher than that in the terrestrial mammals. Foraging efficiency is further improved in Weddell seals as a result of their relatively short hunting events (the dives), the exceptionally low energetic costs of diving, and their ability to acquire multiple energy-dense prey items (fish) in a single dive (Williams and Yeates 2004). Thus, despite the temporal and spatial separation of oxygen and food resources, marine mammals (pinnipeds and otters) have evolved foraging strategies that are as successful as those of their terrestrial counterparts.

Differences in foraging efficiency attributable to foraging style (single vs. multiple prey items) persist even when foraging costs and efficiencies are balanced across a full day (Williams and Yeates 2004). Such scaling is necessary because the wild dog and the lion typically forage daily or within a few days of feeding (Schaller 1972; Estes 1991), while sea otters and Weddell seals forage repeatedly during the day (Ralls et al. 1995; Davis et al. 1999). Comparisons of daily energy intake with field metabolic rate measurements suggest that the terrestrial carnivores balance their energetic costs on a daily to supradaily scale, sea otters forage to meet their daily energy requirements, and Weddell seals meet their daily energy requirements in the course of a few dives but continue to forage (Williams and Yeates 2004). This ability to acquire more than twice their caloric needs each day is especially advantageous for seals when exploiting patchy and ephemeral prey resources and is central to their ability to fast for long periods during the breeding season.

Downtime: Saving Energy When Not Foraging

In contrast to marine and terrestrial carnivores that feed fairly regularly, the time between foraging bouts in snakes that utilize a sit-and-wait strategy can be weeks or months. At the start of these periods of digestive inactivity, snakes effectively shut down gut processes by reducing intestinal mucosa and performance, thereby lowering their metabolism (Secor and Diamond 1998, 2000). Consequently, when prey is captured, gut processes must be elevated rapidly to digest a meal that may be as large as the predator itself. Laboratory studies have demonstrated that snakes exhibit numerous and dramatic physiological responses during the regulation of their gut performance and that the magnitude of these responses varies in response to meal size and feeding frequency.

For example, sit-and-wait-foraging sidewinder rattlesnakes (*Crotalus cerastes*) feed at 1–2-mo intervals in the wild and after feeding double their intestinal mass and increase their mass-specific metabolic and intestinal nutrient uptake rates five- to 10-fold (Secor and Nagy 1994; Secor et al. 1994). In contrast, frequently feeding snakes exhibit a more modest postprandial response and increase intestinal mass and transport by only 50% (Secor and Diamond 2000). This is more similar to the response of mammals, which regulate gut performance over a narrow range during their frequent feeding and fasting cycles (Secor and Diamond 1998).

For all species, the rapid remodeling of digestive processes is triggered by hormonal and luminal signals. In the Burmese python (*Python molurus*), feeding causes an increase in several digestive hormones, including GIP, glucagon, cholecystokinin, and neurotensin (Secor et al. 2001). The postprandial morphological response includes hypertrophy of the enterocytes, lengthening of the villi, and a fourfold increase in the length of the microvilli (Secor et al. 2000b; Starck and Beese 2001). In combination, these trophic responses generate a rapid increase in the luminal surface area of the intestinal epithelium, which partly explains the five- to 20-fold increase in nutrient transport (Secor and Diamond 1995). In addition to increased surface area, the upregulation of intestinal nutrient transport may also be aided by increases in transporter densities and activities.

In contrast to most terrestrial vertebrates, which ingest crushed or fragmented meals, snakes swallow their prey intact. This places a significant functional and metabolic burden on the snake's stomach. For the Burmese python, the digestion of a rodent meal (25% of body mass) stimulates the rapid and continuous production of HCl, which results in gastric pH dropping from 7.5 to 1.5 within 48 h and is sustained until the meal has completely passed from the stomach (Secor 2003). For the python, this cost accounts for more than half of the specific dynamic action associated with the meal (Secor 2003). Feeding also induces significant increases in liver and kidney mass and performance (Secor and Diamond 2000), as well as

a fivefold increase in ventilation and cardiac output and an eightfold increase in intestinal blood flow (Secor et al. 2000*a*; Secor and White 2003).

Clearly, infrequently feeding snakes exhibit dramatic swings in physiological performance with each meal. These responses are designed to conserve energy during extended periods of fasting and maximize the absorption of energy during digestion. In spite of the added cost of gut upregulation with each meal, infrequently feeding snakes reduce their time-averaged daily energy expenditure by downregulating their guts during their extended periods of fasting (Secor 2001). In contrast, the optimum strategy for frequently feeding organisms is to maintain elevated digestive function while fasting, because the costs associated with reactivating the gut outweigh the benefits of reduced tissue maintenance (Secor 2001). These findings illustrate the adaptive interplay between foraging and feeding habits and the capacity to which digestive performance is regulated.

Taking Time: Developing the Physiology for Foraging

The costs and benefits of foraging activities depend in part on the experience and ability of the predator. Juvenile or naive foragers often experience higher costs and lower success rates than older conspecifics, and this can influence their selection of prey and habitat (Burns 1999). Within the marine environment, air-breathing predators are limited to those prey items that they can access during the course of a single breath-hold dive. To maximize dive time, animals have increased the amount of oxygen that can be stored in tissues and reduced the energetic costs of diving (Kooyman 1989). However, neonatal marine mammals have oxygen stores that are significantly smaller than those of adults, when judged on a mass-specific basis (Burns et al. 2004). Therefore, a critical component of ontogenetic development is the upregulation of tissue oxygen stores. Such upregulation must occur relatively quickly in capital-provisioned pups, which are nursed for a period of days to weeks, as compared to income-provisioned pups, which are dependent on maternal care for a period of months to years (Kovacs and Lavigne 1986, 1992).

However, there were strong similarities in the pattern of development in blood and muscle oxygen stores during the nursing and postweaning period in one capital-provisioned (harbor seal *Phoca vitulina*) and one income-provisioned species (Steller sea lions *Eumetopias jubatus*; Burns et al. 2004). Rather than increasing constantly with age, as expected, mass-specific blood oxygen stores declined in the days postpartum and increased only late in the lactation period. The decline was driven by a reduction in hematocrit and hemoglobin that was not ameliorated for weeks (harbor seals) to months (Steller sea lions). Similarly, myoglobin concentrations did not increase during the lactation period in harbor seals and increased only slightly with age in the slower-growing Steller sea lions. Thus, both species were weaned with oxygen reserves that were smaller than those of adults, despite the large difference in the length of the lactation period (4 wk vs. 12–24 mo; Burns et al. 2004).

One reason that nursing marine mammals might experience early declines in hemoglobin and hematocrit and delay development of myoglobin reserves is a limitation in iron intake. Rapidly growing terrestrial neonates that subsist solely on an iron-poor milk diet often manifest a "developmental anemia" that is similar in appearance to that seen in both sea lions and harbor seals (Halvorsen and Halvorsen 1973; Fowler 1986). In addition, measures of iron status (serum ferritin, total iron binding capacity, saturation levels) in harbor seal (Burns et al. 2004) and northern fur seal pups (Mazzaro et al. 2004) suggest that iron is in high demand but poorly available (Finch and Huebers 1982; Ponka 1997). Because iron is necessary for heme production, low iron intake could limit the production of hemoglobin and myoglobin until such time as intake increased or growth slowed. Because phocids grow more rapidly and over a shorter period of time than otariids, it is not surprising that harbor seals were weaned with lower oxygen reserves relative to adult values than were Steller sea lions (Burns et al. 2004).

If iron kinetics influences oxygen store development, then foraging activity in the days and weeks postweaning may be critical for the completion of physiological development. For both Steller sea lions and harbor seals, significant increases in heme stores did occur after diving and/or foraging activity increased (Burns et al. 2004). However, for most phocids, foraging does not occur immediately after weaning but instead occurs only after a postweaning fast that lasts from days to weeks (Kovacs and Lavigne 1986; Muelbert and Bowen 1993). During this period of mass loss, mass-specific body oxygen stores and the ability to regulate metabolic processes increase (Thorson 1993; Zenteno-Savin 1997; Kohin 1998; Noren et al. 2005). Such an increase in oxygen stores requires reallocation of iron reserves either between previously synthesized heme molecules or between tissue ferritin stores and heme production. Because the majority (>80%) of a body's iron is stored in the erythron (van Eijk and de Jong 1992) and there is little change in mass-specific blood volume as animals fast, it seems most likely that iron is reallocated from the erythron into myoglobin.

Regardless of the source of the iron, most phocid pups do not begin to forage until oxygen stores have reached ~2/3 those of adults (Thorson 1993; Burns and Castellini 1996; Burns et al. 2000, 2004; Noren et al. 2005), suggesting that there is a minimum threshold of maturity below which foraging cannot be efficiently sustained. Thus, the postweaning fast may allow phocid pups to reallocate iron stores so that they can begin to forage. However, because final completion of physiological development occurs only after foraging activity begins, newly independent phocid pups may need to quickly develop foraging skills in order to acquire the nutrients necessary to complete the maturation process. In contrast, newly weaned otariids are much more physiologically mature (80%–90% adult values;

Richmond 2004) and may have previous foraging experience (Merrick and Loughlin 1997), both of which would allow for increased behavioral flexibility for newly independent juveniles.

Balancing Time: Resource Allocation and Environmental Variability

Resource allocation decisions can be made at the level of a foraging event, such as the need to balance oxygen reserves with dive duration in marine mammals (Kooyman et al. 1980) or the decision to downregulate gut performance in snakes (Secor 2001). Alternatively, they can be considered in the longer term and with respect to the effect that foraging has on the overall condition of the animal. In species with determinate growth, such as mammals, excess energy and nutrients can be allocated between growth, fattening, and production. However, many animals live in seasonal and/or unpredictable environments and experience periods when available food resources are inadequate to support nutritional requirements (Owen-Smith 2002). Under these conditions, animals lose mass and, if stored fat reserves are insufficient, may die of starvation. While it might seem that animals should store as much fat as possible when energy is plentiful, this may not be the best solution, particularly if there are costs of acquiring and carrying this fat, such as reduced ability to escape predators (Witter et al. 1994), increased costs of locomotion or foraging, or protracted delays in achieving sufficient size for important life-history events such as reproduction or migration.

To determine how much of the surplus resources gained while foraging should be diverted to body fat rather than structural growth or reproduction, we used stochastic dynamic programming (Mangel and Clark 1988; Clark and Mangel 1999) to model the effects of habitat quality, age, and current condition on the resource allocation decisions of large herbivores (Owen-Smith 2004). Our results suggest that because of the costs of carrying fat reserves, fully grown but nonreproductive animals should store the minimum amount of fat needed to get through the adverse season and deposit this fat as late as possible (Owen-Smith 2004). Thus, peak condition (% lipid) should occur at the end of the benign season rather than during the peak of food availability. In addition, where there is greater environmental variability, fat reserves should be larger and should be acquired earlier and carried longer (Owen-Smith 2004). Model predictions agree with observations indicating that the set point for fat reserves varies in response to season, food availability, and sex (Sinclair and Duncan 1972; Mrosovsky and Prowley 1977; Owen-Smith 1988) and that animals from areas with few predators carry larger fat reserves than conspecifics in areas with abundant predators (Tyler 1987).

In contrast to adults, young, growing animals must balance the benefits of fat stores against the costs of growth. The optimal strategy for juvenile growth is to reach the size needed for reproductive maturity as soon as possible by reducing lipid storage (Owen-Smith 2004). However, because lipid stores are necessary to survive periods of low productivity, juveniles may delay growth in lean body mass so that fat reserves can accumulate, and this delay would be more evident where there is greater environmental variability (Owen-Smith 2004). These trade-offs in allocation between growth and storage could explain why survival rates for juvenile ungulates are lower and more variable between years than those of adults (Gaillard et al. 2000).

In combination with previous work, these results highlight the fact that dynamic state–dependent models can be used to test hypotheses about a wide range of life-history questions and to provide insight into the physiological connections between foraging behavior and population dynamics. Contrary to the projections from optimal foraging models that ignore environmental variability (Belovsky 1986), animals should not always operate as rate maximizers for energy or nutrient gains. Gaining energy and the material constituents of biomass provides the power to grow faster, survive better through adverse periods, and reproduce more successfully, but not in all places and at all times.

Digestion Time: Biochemical Indices of Foraging in Free-Ranging Animals

While ingestion events like those by infrequently feeding snakes are not difficult to detect, such is not the case in all animals. For most predators, ingestion events are difficult to observe, and diet must be inferred from recovered stomach or scat contents or some other sample obtained from the animal in question. Short-term samples, such as scats and stomach contents, can be biased because they contain information on only the most recent meal, and certain prey may not be represented in recovered parts (Aram and Naya 2003). New techniques that integrate diet over a longer time frame have been developed and include recovery of DNA from scats (Deagle et al. 2005), analysis of stable-isotope signatures in predator and prey (Burns et al. 1998), and the qualitative or quantitative analysis of fatty acids in lipid samples recovered from the predator (Iverson et al. 2004). Fatty-acid analysis has proven to be a very powerful tool for understanding the diet of many marine predators but has largely been used in species that have large lipid reserves that can be easily sampled by biopsy. However, lipid can also be recovered from serum samples, and recent work in black-legged kittiwakes (*Rissa brevirostris*) has demonstrated that blood serum fatty acids also accurately reflect known diets (Bargmann et al. 2004). In contrast to blubber samples, which integrate diet over relatively long periods (weeks to months), blood lipids reflect the diet over a shorter period of time (days to weeks) and therefore provide more information about the most recent diet. Because blood sampling is simple and relatively noninvasive and small volumes of blood serum fatty acids can be accurately analyzed by mass spectrometry, these results

offer a new tool to scientists interested in studying the foraging ecology of small, or otherwise difficult to handle, animals.

While fatty-acid analysis offers potential for understanding the foraging behavior of animals, tissue and serum lipids are a combination of dietary lipids ingested over the past days to weeks. Therefore, the analysis of fatty-acid signatures does not reveal information about when in the past foraging actually occurred. On the other hand, obtaining blood samples from free-ranging animals while they are foraging, in order to follow digestion biochemistry in real time, is essentially impossible in most systems. This is especially true for large terrestrial mammalian carnivores (e.g., large cats, bears). However, there are some marine mammals that offer a unique opportunity to follow feeding biochemistry in the field.

The Weddell seal (*Leptonychotes weddellii*), which lives in Antarctic waters, is one such example. These animals can be catheterized and then allowed to dive freely from an artificial hole drilled in the sea ice, allowing researchers to collect post-dive blood samples without altering natural behaviors (Kooyman et al. 1980; Guppy et al. 1986). While it has long been recognized that seal blood would become lipemic (cloudy because of high lipid levels) during foraging bouts, only recently did we realize that because marine mammals use lipid as their primary metabolic fuel (Davis 1983; Davis et al. 1992), the pattern of appearance and clearance of lipids and their by-products (cholesterol, triglyceride, glycerol, and chylomicron remnants) could be used to study digestive physiology.

Work on the digestive physiology of diving Weddell seals indicates that the blood chemistry begins to show the markers of lipid digestion about 1.5 h after the initiation of a diving bout. During a foraging bout, total lipids, triglycerides, and glycerol increase, while cholesterol remains constant and blood glucose decreases (M. A. Castellini, unpublished data). The increase in glycerol is of particular interest because it is common to both carbohydrate and lipid metabolic pathways (Davis 1983; Davis et al. 1992). When seals rest at the surface at the end of a foraging bout, these biochemical markers begin to return to baseline (resting, postabsorptive) levels. However, seals routinely initiate another foraging bout before resting levels are achieved (M. A. Castellini, unpublished data). Because observed changes in blood chemistry did not occur after diving bouts during which seals were not successful (i.e., their blood did not become lipemic), these changes cannot be attributed solely to exercise and instead must be due to digestive processes. Upcoming studies that use labeled lipids, proteins, and carbohydrates to measure metabolite production and degradation rates will shed light on how these compounds are used to support metabolism in an actively foraging animal. Overall, this work will provide the first estimates of the digestive biochemistry of a naturally foraging large mammalian carnivore, terrestrial or marine.

Conclusions

The purpose of this symposium was to examine how foraging energy (both costs and gains) is partitioned over time. "Time," in this case, ranged from evolutionary time (how different animals are designed to most efficiently forage), to long, lifetime periods (development of foraging ability and growth), to short-duration feeding bouts, and ultimately to the minutes to hours following ingestion (metabolic and biochemical changes). What conclusions can be drawn from this type of wide-ranging analysis?

First, these studies make it clear that there are evolutionary, physiological, and biochemical "limits" within which even foraging behavior is constrained. Whether these limits are imposed by the environment or the physical abilities of the animals is not as important as the ability of the animal to adapt to such limits. All the symposium speakers highlighted the fact that animals have adapted: seals forage extremely efficiently, snakes alter their gut morphology, physiology, and biochemistry at a variety of temporal scales, and ungulates alter the amount and duration of fat storage, all in response to variations in the availability of food resources.

The temporal pattern of food availability also appears to have influenced digestive physiology across much larger timescales. For example, lipid digestion is of extreme importance to marine mammals, because lipids provide the bulk of their caloric intake. Therefore, over evolutionary time, marine mammals have come to rely on protein and carbohydrate metabolism for structural growth and metabolic control but not for calories. Thus, seal pups must develop their diving ability in the face of potential protein limitation (iron, hemoglobin, and myoglobin chemistry) but simultaneously develop the ability to process massive amounts of lipid. Once physiologically mature, pinnipeds possess the biochemical abilities to quickly and efficiently process and store much larger amounts of lipid than terrestrial animals, so that periods of low food availability can be overcome. Similarly, intermittently foraging snakes have evolved strategies to reduce digestive costs during periods of low food availability, but when faced with abundance, they can quickly upregulate gut function to process large loads, options not available to frequently feeding species experiencing food shortages.

Second, the talks emphasized that within the evolutionary, physiological, and biochemical foraging limits described above, animals have the behavioral flexibility to optimize their foraging decisions. For example, terrestrial and marine predators may forage in bouts (or on multiple items at once) or during single events (or on single prey items), and the optimal strategy will be influenced by the temporal and spatial patterns of food availability and by the physiological capabilities of the predator. Thus, young animals may partition themselves into a foraging environment where they can physically obtain their food easily even though "better" food sources may be nearby, or they may allocate food resources differently than older, more mature animals.

In combination, these concepts can be integrated into a single emergent theme: animals cope with variability in the resources available to them across a range of time frames, and their responses are evident in physiology, behavior, and life-history strategies. Thus, diving seals seem to forage extremely efficiently compared with terrestrial carnivores. But they have to, because there are times of the year when reproduction or molt precludes foraging, and the surplus energy gained by efficient foraging must see them through these fasting periods. In contrast, most terrestrial carnivores do not store fat because they could not hunt effectively if they carried the extra mass, and they therefore must secure relatively large amounts of food every few days. Snakes have adapted toward another extreme, saving energy by eliminating basic digestive tissues during long periods of fasting and paying the costs of restoring them when needed. Over longer time periods, there are life-history stages when young animals have to face the challenge of growing from a suboptimal body size toward adulthood while perhaps simultaneously coping with inadequate mineral and/or nutritional reserves, which therefore increase the risks of mortality through predation or starvation. The final talks in the symposium emphasized that as new and exciting research tools become available, we will be better able to study the interplay among behavioral, physiological, and environmental factors that influence foraging decisions across a range of animals and environments. This will place the biology of natural foraging at the forefront of new discoveries in the field of comparative animal physiology.

Acknowledgments

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