

Constraints on active-consumption rates in gray wolves, coyotes, and grizzly bears

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Abstract: Predators' feeding strategies lie on a continuum between energy maximizers, who maximize the energy obtained from a patch of food, and time minimizers, who minimize the time required to get a fixed ration of food from a patch. Carnivores that feed on large prey should adopt a time-minimizing strategy by maximizing their active-consumption rate (ACR) if they evolved under conditions of high competition from group members, and conversely adopt an energy-maximizing strategy if they evolved under conditions of low competition from group members and were thus able to monopolize their prey. By provisioning animals with large pieces of ungulate carcasses, we measured ACR for captive gray wolves (*Canis lupus*), coyotes (*Canis latrans*), and grizzly bears (*Ursus arctos*). In accordance with a conspecific-competition hypothesis, ACR increased with sociality. Other factors influencing ACR included subject body mass and food type, ACR being significantly faster on muscle and organs than on bone and hide. Measuring ACR is crucial to empirical and theoretical studies assessing foraging decisions and may be used as an indicator of an animal's competitive environment.

Résumé : Chez les prédateurs, les stratégies alimentaires se situent dans un continuum entre, d'une part, les maximiseurs d'énergie qui maximisent l'énergie qu'ils peuvent soutirer d'une source de nourriture et, d'autre part, les minimiseurs de temps qui minimisent le temps requis pour recueillir une quantité donnée de nourriture à la source alimentaire. Les carnivores qui se nourrissent de proies de grande taille devraient adopter une stratégie de minimisation du temps en maximisant leur taux de consommation active (ACR) s'ils ont évolué dans des conditions où la compétition entre les membres du groupe est forte et, inversement, une stratégie de maximisation de l'énergie s'ils ont évolué dans des conditions où il y a peu de compétition de la part des membres du groupe et où ils ont donc le monopole de leurs proies. Nous avons donné de grands morceaux de carcasses d'ongulés à des loups gris (*Canis lupus*), des coyotes (*Canis latrans*) et des grizzlis (*Ursus arctos*) en captivité et nous avons mesuré ACR. En accord avec l'hypothèse sur la compétition conspécifique, ACR augmente en fonction de la socialité. Parmi les autres facteurs qui peuvent influencer ACR, il faut mentionner la masse du sujet et son type de nourriture; dans le cas de muscles et d'organes, ACR est plus élevé que dans le cas des os et de la peau. La mesure d'ACR est essentielle à l'évaluation des décisions en matière d'alimentation, dans les études empiriques aussi bien que dans les études théoriques, et elle peut servir d'indicateur de l'environnement compétitif d'un animal.

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Introduction

Optimal-foraging theory predicts that foragers attempt to maximize their energy-intake rates (Charnov 1976). Unfortunately for comparative biologists, measures of intake rate are inconsistent across studies. Many consider intake rate to be a long-term average of net energy intake, i.e., over the time that the animal may spend time searching, chasing, consuming, and (or) digesting prey (Stephens and Krebs 1986). The

active-consumption rate (ACR), defined as the mass of food consumed per unit time spent actively feeding, is often implicit in net measures, yet may be more appropriate as a primary measure of feeding performance when, for example, food patches are large and concentrated. Diet-selection studies on feral goats, for instance, have revealed that these animals choose grass species that maximize their ACR over variants that are more nutritious (Illius et al. 1999). Grizzly bears (*Ursus arctos*) feeding on fruit diets have been shown to lose mass if the density of berries is not high enough to meet their maximum ACR (Rode and Robbins 2000).

Predators feeding on large prey may similarly seek to maximize ACR rather than overall energy intake (Holekamp et al. 1997). Recent modeling efforts, however, illustrate the paucity of existing information on ACR for carnivores (Carbone et al. 1997, 1999). For example, Carbone and colleagues (1997) used an estimate of wild dog (*Lycaon pictus*) ACR extrapolated from Schaller (1972), who describes one dog with a full gut leaving a carcass 8 min after a kill. Although this information is useful, knowledge of how ACR varies within and between species according to size, age, sex, and feeding strategy of the carnivore and prey meat type (e.g., bone vs. muscle) is necessary for a fine-grade understanding of predators'

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foraging decisions. As an example of this fine-grade approach, ACR may be used in conjunction with field observations of time spent at a carcass to determine the approximate number of calories obtained by an animal in a given feeding bout (Henschel and Tilson 1988). Models examining energetic or predator-prey interactions can then incorporate ACR into more accurate measures of assimilation efficiency and interaction strength.

ACR may also be an important predictor of feeding strategy. Predators may be thought of as either energy maximizers, who maximize the amount of energy obtained from a patch, or time minimizers, who minimize the time required to get a fixed ration of food from a patch (Schoener 1971). Griffiths (1980) suggested that these strategies lie on a continuum and correlate with the group size of the species concerned. As group size increases, competition between group members similarly increases, making the time-minimizing strategy more beneficial (i.e., intragroup competition influences the feeding rate). Carnivores living in large groups, such as spotted hyenas (*Crocuta crocuta*), African lions (*Panthera leo*), wild dogs, and gray wolves (*Canis lupus*), feed quickly in a scramble competition for food, then leave the immediate area (Kruuk 1972; Mech 1970; Schaller 1972). Conversely, solitary animals, such as leopards (*Panthera pardus*) and grizzly bears, often cache large prey and may stay with them for some time (Schaller 1972; Craighead et al. 1995).

Social species often gorge themselves at the expense of inefficient digestion (Mech 1970), whereas solitary species may take more time to feed and more efficiently digest their food. As an example of intraspecific variation in ACR, Tilson and Hamilton (1984) showed that spotted hyenas in East Africa, which live in relatively large groups, consumed prey much more rapidly than did hyenas in the Namib Desert, which live in relatively small groups. While all species on the feeding-strategy continuum should seek to maximize their energy intake, species living in large groups are predicted to have a high ACR, species living in small groups an intermediate ACR, and solitary species a low ACR. This relationship arises as a result of the differences in selection pressure on ACR imposed by differing levels of intraspecific competition. Interspecific competition may also be an important factor driving ACR (Carbone et al. 1997), but is generally thought to be minor compared with intraspecific competition.

The present study was conducted in order to measure ACR in three common North American carrion feeders: gray wolves, who are highly social and live in large packs of 2–36 individuals (Mech 1970; Mech et al. 1998); coyotes (*Canis latrans*), who are moderately social and live in small packs of 2–10 individuals (Bekoff and Wells 1980; Gese et al. 1996), and grizzly bears, who are solitary (Craighead et al. 1995). We tested how ACR varies with predator size, age, and sex and prey meat type. We then investigated how ACR varies among species according to the degree of sociality.

Methods

Coyote feeding trials were conducted in May 2001 at the Logan, Utah, field station of the United States Department of Agriculture National Wildlife Research Center. Coyotes were caged in 0.1-ha outdoor enclosures. We fed 29 coyotes ranging in age from 2 to 12 years and in mass from 5.6 to

13.7 kg. Food was withheld from subjects for 48 h prior to feeding to ensure a robust appetite. Gray wolf feeding trials were conducted in June 2001 at Mission Wolf, a captive wolf refuge outside of Gardner, Colorado. Wolves were caged in 0.5- to 2.0-ha outdoor enclosures. We fed 15 wolves ranging in age from 6 to 12 years and in mass from 31.8 to 61.3 kg. Food was withheld for 72 h prior to feeding. Grizzly bear feeding trials were conducted in May 2001 at the Grizzly Discovery Center in West Yellowstone, Montana. Grizzly bears were caged in 25-m² indoor enclosures and were rotated into a 0.5-ha outdoor habitat twice a day. We fed 7 grizzly bears ranging in age from 3 to 14 years and in mass from 158 to 425 kg. Food provisions for the bears were cut in half for 24 h prior to the feeding trials. We chose animals who were representative of a wide range of masses and ages and withheld food for a period that was long enough to ensure a robust hunger level. We did not have information on coyote masses until after the feeding trials; however, the majority were very close. All animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Feeding trials consisted of provisioning animals with large pieces of muscle, organ, rib cage, leg bone, and hide from freshly killed mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*). We chose pieces of muscle from the hind and front quarters that were similarly dense and large enough to ensure that subjects would tear at the meat as they would in the wild but not so large as to fully satiate them. Rib cage, leg bone, and hide each had approximately 3 cm of meat on them at the beginning of the feeding trial. We provisioned wolves and grizzly bears with rib cage, leg bone, and hide from elk only. We fed mule deer that had thinner bone and hide to coyotes, but this did not seem to make a difference because coyotes tended to scrape the bone rather than break it. All meat was weighed and fed to the animals individually. Subjects were then timed to the nearest second until they had fully consumed the meat in the case of muscle and organs, or for a preset time until the meat was retrieved in the case of all bones and hide. If meat was retrieved, we weighed the remains and subtracted this mass from the initial mass to calculate the total mass consumed. Feeding time was defined as time spent actively licking, tearing, stomping (grizzly bears stomp ribs to break them), or chewing meat. Time not spent actively feeding on the meat was excluded from feeding time. ACR was then calculated as the ratio of the mass of meat consumed to feeding time in grams per minute. We conducted at least 10 trials per meat type for coyotes and wolves and 7 trials per meat type for grizzly bears. In some cases, however, the sample size was below 10 because of logistical problems with certain animals (e.g., some animals, particularly some wolves, guarded bones when we tried to retrieve them for weighing). We randomized the order in which meat types were fed to each animal. Feeding sessions were conducted over a few days for each species, the intervals between sessions being equal to the withholding times reported above. If an animal was fed multiple meat types in the same day, we took care that the amount of food it received was small relative to its regular daily ration to mitigate the effect of satiation. We did not feed leg bone or organs to grizzly bears because these were unavailable. Wolves did not eat the hide we provided.

We calculated ACR (mean \pm standard error) for each species by meat type; *t* tests were used to compare ACRs between meat types and between the sexes. We used standard linear regression models to determine the effect of carnivore age and mass on ACR.

Results

Coyotes

ACRs did not differ significantly between rib cage, leg bone, and hide or between muscle and organs (Fig. 1, Table 1). Differences in ACR between rib cage, leg bone, and hide and muscle and organs, however, were highly significant ($p < 0.01$). Coyote age was negatively associated with ACR on both rib cage, leg bone, and hide and muscle and organs; however, it was significant only on muscle and organs ($p = 0.02$, $r^2 = 0.38$). Coyote mass was not significant by itself (Fig. 2), but when age was controlled for, there was a positive association between mass and ACR on both rib cage, leg bone, and hide and muscle and organs. Most of the coyotes tested weighed between 10 and 12 kg, which was too small a range to properly explore the effect of mass on coyote ACR. Coyote sex was not a significant predictor of ACR on either muscle and organs or rib cage, leg bone, and hide.

Wolves

As in coyotes, ACR on rib cage and leg bone did not differ significantly, nor did ACR on muscle and organs (Fig. 1, Table 1). Differences between ACR on rib cage and leg bone and muscle and organs, however, were highly significant ($p < 0.01$). Although wolf mass was positively correlated with ACR on all meat types, it was significantly correlated with ACR only on muscle and organs ($p = 0.05$, $r^2 = 0.30$) (Fig. 2). ACR of female wolves was slower than that of males on all meat types but the difference was significant only on muscle ($p = 0.05$). Wolf sex and mass were highly correlated ($r = 0.88$), so that when mass was controlled for, sex was no longer a significant predictor of ACR. ACR slowed with increasing wolf age, but this effect was not significant on any of the meat types.

Grizzly bears

ACRs on rib cage and hide did not differ significantly (Fig. 1, Table 1). Differences between ACR on rib cage and hide and that on muscle, however, were highly significant ($p < 0.01$). Grizzly bear mass was positively correlated with ACR on all three meat types. As a predictor of ACR, it was significant for muscle ($p = 0.02$, $r^2 = 0.67$) (Fig. 2), nearly significant for hide ($p = 0.08$, $r^2 = 0.48$), and not significant for ribs. Grizzly bear age was also a good predictor of ACR ($p = 0.09$, $r^2 = 0.67$) on muscle, but as age was highly correlated with grizzly bear mass ($r = 0.86$), it was not possible to determine the effect of age alone. Of the 7 grizzly bears tested, only 1 was female, so it was not possible to determine the effect of grizzly bear sex on ACR. Furthermore, the female was not an obvious outlier in the data.

Comparisons

Techniques of feeding on muscle were similar among species, with animals using their canines to tear off strips of

Fig. 1. Active-consumption rates (ACRs) for coyotes (A), wolves (B), and grizzly bears (C).

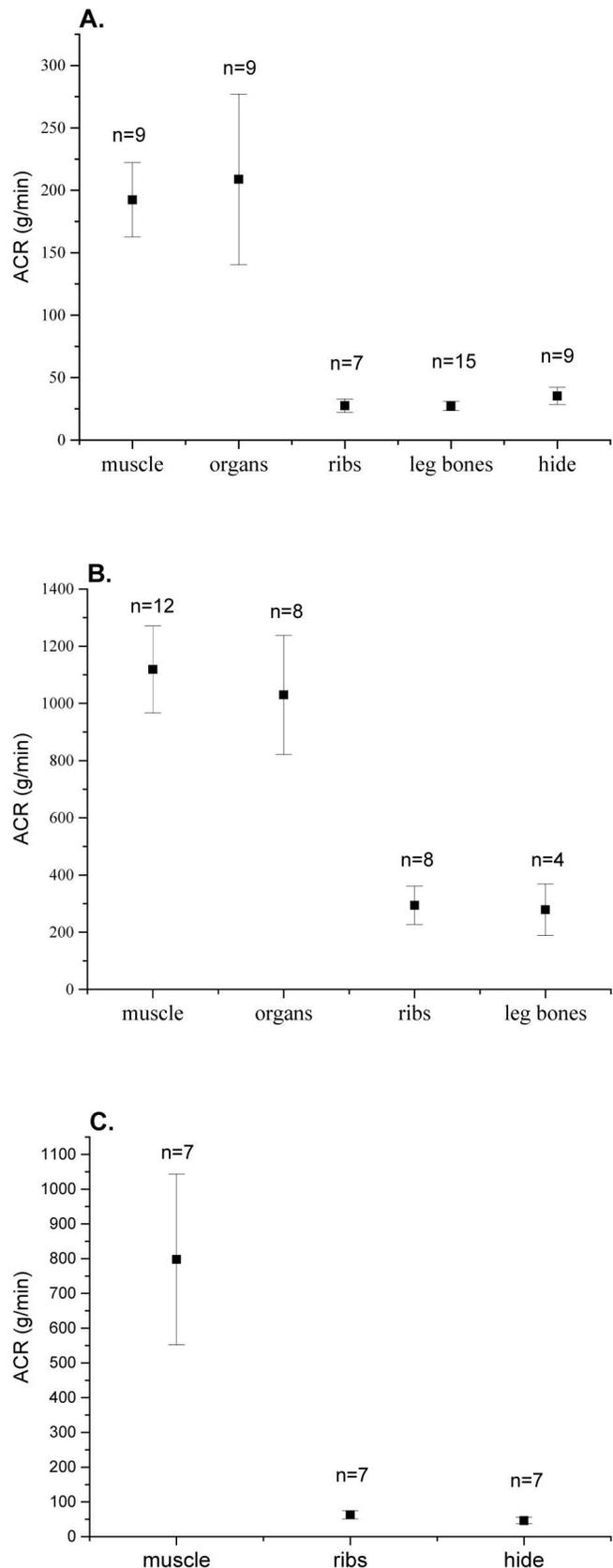


Table 1. ACRs (g/min) by meat type for three carnivore species.

	Coyote	Gray wolf	Grizzly bear
Muscle	192.45 ± 29.75	1118.79 ± 152.10	797.80 ± 245.70
Organs	208.92 ± 68.36	1029.83 ± 208.25	na
Rib cage	27.57 ± 5.52	293.97 ± 67.26	62.82 ± 11.91
Bone	27.37 ± 3.77	278.78 ± 89.79	na
Hide	35.39 ± 6.93	na	46.23 ± 8.64

Note: Values are given as the mean ± SE. There was no significant difference in ACR between rib cage, bone, and hide or between muscle and organs for any of the species. However, differences between ACR on rib cage, bone, and hide and that on muscle and organs were highly significant in all three species ($p < 0.01$).

meat. Additionally, for wolves and grizzly bears, ACR on muscle was significantly predicted by subject mass. Although we suspect that this is also the case with coyotes, we were unable to demonstrate it, owing to the lack of variation in coyote mass. By dividing the ACR for each subject by its mass, we were able to obtain a standardized ACR (ACR/mass) to allow comparison among species. A species' degree of sociality correlated well with its standardized ACR. The standardized gray wolf ACR was faster than the coyote ACR (24.78–17.85 g/(kg·min), $p = 0.07$), which in turn was much faster than the grizzly bear ACR (17.85–2.75 g/(kg·min), $p < 0.01$).

Discussion

When consuming a carcass, wolves eviscerate the organs, feed on the major muscle groups on the hind and front quarters, and then pick the remaining muscle off the ribs, leg bones, and hide (Mech 1970; Carbyn 1983). The skeleton, particularly the larger bones, and some hide usually remain after feeding has finished. ACR on a carcass can be broken down into two distinct periods depending on the stage of consumption of the kill. Our results show that major muscle groups and organs are consumed at similarly high rates, while minor muscle on the bone and hide is consumed at similarly slower rates (Fig. 1). These differences may reflect feeding methods. When presented with muscle, all three species used their canines to tear off strips of meat. Conversely, when presented with bone and hide, they turned their head sideways, chewing and scraping the meat, and occasionally breaking the bone, with their carnassial teeth.

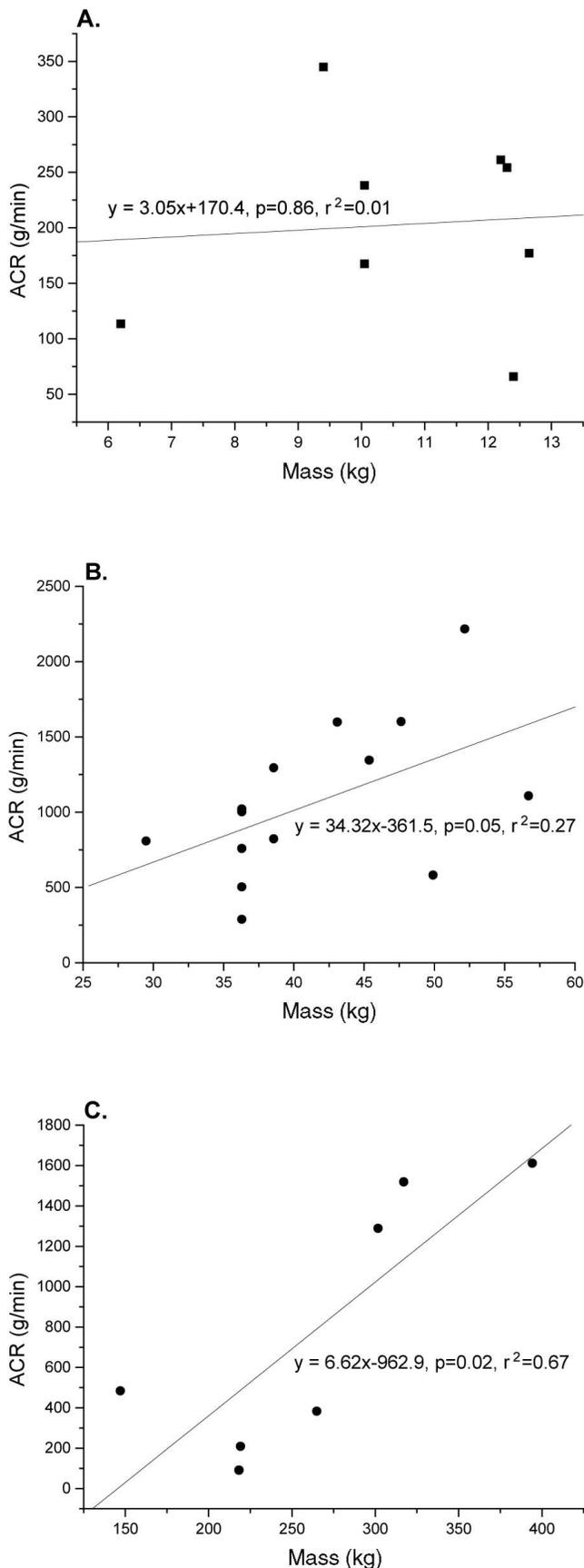
ACR may be combined with field observations to estimate the amount of biomass consumed by an individual or a species at a particular kill site. Field measures of biomass consumed may be derived in two ways. (1) Absolute measures may be obtained by focal sampling of subjects, recording when they are actively feeding and what part of the carcass they are feeding on. Biomass consumed is the time spent feeding on each meat type weighted by ACR on that meat type. (2) Relative measures may be obtained by scan sampling of subjects at regular intervals, recording whether or not they are actively feeding and the stage of consumption of the carcass. Biomass consumed may then be estimated using relative feeding rates between individuals or species and an estimate of available biomass (Henschel and Tilson 1988). Absolute measures are likely to be more accurate than relative measures but may be more difficult to obtain if the carcass is occasionally blocked from view or sampling effort is constrained by other research protocols.

The results presented here suggest that within a carnivore species, ACR is likely to be affected by its mass, age, and sex. As carnivores increase in size, ACR tends to increase (Fig. 2). Female wolves were slower feeders than males but were also smaller, therefore the difference in ACR is most likely due to the sexual size dimorphism in canids. As canids get older they tend to feed more slowly, possibly because of lost or chipped teeth (D. Smith, personal communication). In addition, older animals are more likely to be dominant, which might decrease the effect of intragroup competition on ACR. We did not test the effect of dominance on ACR, but this might be an important factor to consider in future studies. Grizzly bears, conversely, tended to feed more rapidly as they increased in age. However, our sample was not large enough to tease out the effect of age from that of mass on ACR in grizzly bears.

At the proximate level, the differences in ACR between wolves, coyotes, and grizzly bears may be due differences in gut physiology and dentition. For instance, wolves are able to expand their gut capacity in order to consume large quantities of meat (Mech 1970). In addition, the masticatory apparatus of the wolf is adapted for eating food quickly in large packages (Hall 1978). Conversely, grizzly bears have an elongated digestive tract designed for more efficient digestion of vegetation (Herrero 1985). Ursid molars are also longer and flatter than those of canids so that they may grind plant matter more efficiently (Kurten 1976). Grizzly bears' ability to consume and digest vegetation, therefore, may cause a corresponding decrease in their ACR on meat.

Feeding strategy (time minimizing vs. energy maximizing) was a good indicator of ACR, which increased with the degree of sociality of the species. Though our sample of species was small, ACR increased with species-specific group size within taxa (between coyotes and wolves) and between taxa (between canids and bears). At the ultimate level, intensity of competition between group members may drive the observed patterns of standardized ACR. Wolves in the wild feed communally at fresh kills, with as many as 13 animals feeding at once (Mech 1970). Coyotes feed in smaller groups, with no more than 5 individuals feeding at the same time (C.C. Wilmers, personal observation). Grizzly bears feed singly and will generally stay at a carcass for many hours, intermittently feeding and sleeping on the carcass (C.C. Wilmers, personal observation). Preliminary evidence suggests that because of intense competition from conspecifics, wolves have evolved a time-minimizing strategy by maximizing their ACR. Coyotes are also time minimizers, but because competition is less than among wolves because groups are smaller,

Fig. 2. Relationship between subject body mass and ACR on muscle in coyotes (A), wolves (B), and grizzly bears (C).



they feed more slowly. Conversely, grizzly bears, which are solitary and thus do not face competition from group members, are able to monopolize kills and hence have evolved an energy-maximizing strategy for which selection on ACR has been relaxed.

Examination of Schaller's (1972) observation of a wild dog mentioned previously reveals a similar pattern. Assuming that it had a gut capacity of 4.4 kg (Carbone et al. 1997) and a body mass of 25 kg (Gorman et al. 1998), this wild dog would have a minimum standardized ACR of 22 g/(kg·min), which is in accord with the values we have reported for wolves. Wild dogs are also highly social, living in packs of 2–32 animals, with a mean pack size of 9–10 animals (Kruuk and Turner 1967; Schaller 1972), which is similar to average pack sizes reported for wolves (Mech et al. 1998).

There may be other explanations for the patterns that we observed regarding the effect of species-specific sociality on ACR. For instance, the difference in consumption rates between the three species may be due to their position along a dietary specialist–generalist continuum with wolves as specialists, coyotes as moderate generalists, and grizzly bears as the ultimate generalists. Specialists may be able to maximize their ACR on one food type because they are not constrained by other dietary requirements. It is also possible that animals studied in captivity behave differently than their wild counterparts. Predators at a kill in the wild, for instance, are likely to be more vigilant and may engage in competitive interactions with conspecifics. Our study subjects, however, were fed individually. To control for this, our definition of ACR specifically excludes vigilance and intraspecific interactions, which are most likely to vary with increasing competition. Ecologists seeking to measure biomass consumed by predators in the wild may need to be careful, therefore, to discount time spent vigilant and interacting from total time spent at the carcass in order to obtain active-feeding times.

A carcass may be divided into several components with regard to feeding behavior. Our results indicate, however, that from the perspective of ACR, it is not necessary to distinguish between muscle and organs for coyotes and wolves or between rib cage and (or) bones and (or) hide for all three species. In addition, we have shown that ACR on ungulate carcasses may (i) vary with carnivore age and mass, with larger and younger animals tending to feed more quickly in canids and larger and older animals tending to feed more quickly in grizzly bears, and (ii) increase with mean species-specific group size. We have presented a method that may be used in conjunction with field observations to measure biomass consumed and parameterize theoretical models of foraging behavior, energetics, and predator–prey dynamics. In addition, standardized ACR is an indicator of position on the time-minimizing – energy-maximizing continuum and may be indicative of an individual's or species' competitive history.

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