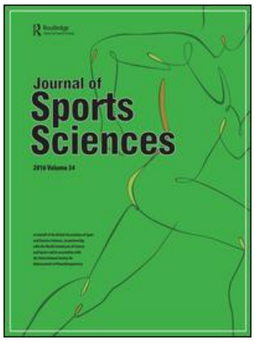

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Dietary protein for athletes: From requirements to optimum adaptation

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Abstract

Opinion on the role of protein in promoting athletic performance is divided along the lines of how much aerobic-based versus resistance-based activity the athlete undertakes. Athletes seeking to gain muscle mass and strength are likely to consume higher amounts of dietary protein than their endurance-trained counterparts. The main belief behind the large quantities of dietary protein consumption in resistance-trained athletes is that it is needed to generate more muscle protein. Athletes may require protein for more than just alleviation of the risk for deficiency, inherent in the dietary guidelines, but also to aid in an elevated level of functioning and possibly adaptation to the exercise stimulus. It does appear, however, that there is a good rationale for recommending to athletes protein intakes that are higher than the RDA. Our consensus opinion is that leucine, and possibly the other branched-chain amino acids, occupy a position of prominence in stimulating muscle protein synthesis; that protein intakes in the range of 1.3–1.8 $g \cdot kg^{-1} \cdot day^{-1}$ consumed as 3–4 isonitrogenous meals will maximize muscle protein synthesis. These recommendations may also be dependent on training status: experienced athletes would require less, while more protein should be consumed during periods of high frequency/intensity training. Elevated protein consumption, as high as 1.8–2.0 $g \cdot kg^{-1} \cdot day^{-1}$ depending on the caloric deficit, may be advantageous in preventing lean mass losses during periods of energy restriction to promote fat loss.

Keywords: *Leucine, hypertrophy, protein turnover*

Introduction

While the net rates of protein synthesis and degradation, collectively referred to as "turnover", are relatively high in humans, the net loss (synthesis minus breakdown) of amino acids is relatively low. For example, whole body protein breakdown might be 280 $g \cdot day^{-1}$ in a 70 kg male with 28–32 kg of skeletal muscle tissue. Whole body protein synthesis would be about 280 $g \cdot day^{-1}$ also; however, there are transient periods in which protein breakdown exceeds synthesis and in that time there is a net loss of amino acids necessitating the consumption of protein to replace losses. Those losses are typically about 40–60 $g \cdot day^{-1}$ for a sedentary person weighing 70–90 kg and it is debatable what the losses would be in athletes, be they aerobically trained or resistance trained. The current US and Canadian RDA and Australian RDI tell us that a daily protein intake somewhere between 0.75 and 0.80 $g \cdot kg^{-1}$ will meet the needs of about 98% of the population. The most recent American College of Sports Medicine position stand (Gerovasili et al., 2009) on dietary practices for athletes recommends a protein intake of 1.2–1.7 $g \cdot kg^{-1} \cdot day^{-1}$ for endurance- and resistance-trained athletes. All of the above recommendations are based on data from studies of nitrogen balance. From a physiological perspective, to be in nitrogen – or protein – balance means only that protein (nitrogen) intake is balanced by protein (nitrogen) loss. It is hard to imagine what variable an athlete or their coach might believe is associated with being in nitrogen balance, least of all performance. It is also well acknowledged that the nitrogen balance technique has serious technical drawbacks, which may result in requirements that are too low. The reader is referred to the most recent WHO/FAO/UNU technical report (Sakuma et al., 2009) for a detailed and in-depth discussion of the various drawbacks of the nitrogen balance approach.

Despite the technical problems of nitrogen balance, a number of studies have attempted to define what protein intakes would be required to achieve

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a state of nitrogen balance, and thus define an athletic protein requirement, in athletes (Friedman & Lemon, 1989; Lemon, Tarnopolsky, MacDougall, & Atkinson, 1992; Tarnopolsky, MacDougall, & Atkinson, 1988). Data from these studies leads to the conclusion that the protein needs of athletes can be as high as twice the RDA/RDI (Friedman & Lemon, 1989; Lemon et al., 1992; Tarnopolsky et al., 1988). At the same time, a number of longitudinal studies have reached the conclusion that exercise training in novices actually reduces protein utilization and requirements due to reduced activation of amino acid oxidation/catabolism in endurance athletes (McKenzie et al., 2000), or that resistance exercise induces a more efficient use of amino acids arising from muscle protein breakdown (Hartman, Moore, & Phillips, 2006; Moore et al., 2007). What is more important perhaps than debating what nitrogen balance means for an athlete is to look at protein from a functional perspective and to try and recognize that an ''optimal'' intake for athletes might exist that is not predicated on merely satisfying a minimal requirement and thus being in nitrogen balance. It is also recognized that such an intake is not easy to define. The function that athletes care most about is optimal performance in their sport of choice. Often improvements in performance will involve gaining muscle mass and potentially also losing fat mass, as a high lean-to-fat body weight ratio is desirable in several sports. With this framework in mind, we can look at specific situations where protein can act as a substrate for the synthesis of new muscle proteins, leading eventually to net muscle accretion or to the repair of excessive protein damage, and at strategies to aid in fat mass loss while still maintaining lean mass. Thus, the goal of this review is to provide some guidance as to what an athletic ''optimal'' protein intake might be.

The role of protein in training-induced adaptation

Muscle mass is normally fairly constant during adult life up to the fourth or fifth decade, when the slow process of sarcopenia is thought to begin (Evans, 1995). The maintenance of muscle mass is a balance between muscle protein synthesis (MPS) and muscle protein breakdown (MPB). The algebraic difference between MPS and MPB, to yield net muscle protein balance (NPB), is the operative variable determining gain or loss of muscle mass (Burd, Tang, Moore, & Phillips, 2009). Obviously, from the standpoint of obtaining an optimum adaptation, athletes look to maximize the adaptive responses to their training bouts by maximizing their NPB. This is accomplished through the synergistic action of both exercise and amino acid/protein ingestion to promote increases in MPS (Moore, Phillips, Babraj, Smith, & Rennie, 2005; Moore et al., 2009b). The key processes underlying these adaptations, involving gene transcription, protein signalling, and translation initiation, are too complex and tangential to the main focus of this review; however, the reader is referred to several reviews on these topics for more in-depth discussion of these mechanisms (Hundal & Taylor, 2009; Mahoney & Tarnopolsky, 2005; Rennie, Wackerhage, Spangenburg, & Booth, 2004; Sarbassov et al., 2004).

Protein ingestion following exercise reduces indices of damage such as release of creatine kinase (Greer, Woodard, White, Arguello, & Haymes, 2007; Rowlands, Thorp, Rossler, Graham, & Rockell, 2007; Rowlands et al., 2008; Valentine, Saunders, Todd, & St. Laurent, 2008). How dietary protein ingestion might affect muscle damage is unknown. There is some indication that post-exercise protein feeding might support an enhanced performance (Cockburn, Stevenson, Hayes, Robson-Ansley, & Howatson, 2010; Rowlands et al., 2008; Saunders, Moore, Kies, Luden, & Pratt, 2009), but no plausible mechanism for this effect is readily available and not all data support such a conclusion (Cermak, Solheim, Gardner, Tarnopolsky, & Gibala, 2009; van Essen & Gibala, 2006). What cannot be ignored, however, is the fact that protein consumption is necessary for MPS to be stimulated to result in a positive NPB. Athletes engaged in resistance exercise would no doubt find benefit in repeated periods of positive protein balance to eventually allow for muscle protein accretion and subsequent hypertrophy to occur. It is less clear what benefit endurance-trained athletes may derive, but it is not unreasonable to suggest that mitochondrial protein synthesis would proceed at a higher rate with ingestion of protein versus no protein (Wilkinson et al., 2008). The supposition would then be that endurance athletes may experience a greater training-induced increase in mitochondrial volume and enhanced adaptation in response to training, but such a thesis has not been tested. A recent paper did find that immediate post-exercise supplementation with protein versus carbohydrate did result in greater improvements in peak oxygen uptake in older men (Robinson, Turner, Hellerstein, Hamilton, & Miller, 2011); however, how protein accomplished this is uncertain.

Protein serves both as a substrate and a trigger for adaptation after both resistance and aerobic exercise. If protein provision in close temporal proximity to exercise promotes a better adaptation (i.e. greater muscle mass gain or greater gains in oxidative capacity), then this would serve as a basis for a framework in which we can begin to discuss an optimum protein intake for athletes. There is evidence to support this concept in resistance training studies (Cribb & Hayes, 2006; Hartman et al., 2007; Holm et al., 2008), but not for aerobic-based training. However, inherent in the concept that protein consumption promotes training is the need to focus on protein intakes that create optimum adaptation rather than those tied merely to nitrogen balance. Viewed from this perspective, there are important messages for athletes in terms of quantity, timing, and quality of protein intake in relation to the training stimulus.

What quantity of protein should athletes consume?

The US Dietary Reference Intakes (DRI) specify a daily dietary protein intake for all individuals aged 19 years and older of 0.8 g $\cdot$ kg^{-1} (Institute of Medicine, 2005). This recommended dietary allowance (RDA) is cited as adequate for almost all persons. This amount of protein would be considered by many athletes as the amount to be consumed in a single meal, particularly for strength-trained athletes. There do exist, however, published data to suggest that individuals habitually performing resistance and/or endurance exercise require more protein than their sedentary counterparts (Friedman & Lemon, 1989; Lemon et al., 1992; Tarnopolsky et al., 1988, 1992). The RDA values for protein are clearly set at "the level of protein judged to be adequate ... to meet the known nutrient needs for practically all healthy people" (Institute of Medicine, 2005). The RDA covers protein losses with margins for inter-individual variability and protein quality, but the notion of consumption of "extra" protein above these levels to cover increased needs due to physical activity is not considered.

Studies of protein requirements in athletes have shown an increased requirement for protein in strength-trained (Lemon et al., 1992; Tarnopolsky et al., 1988, 1992) and endurance-trained athletes (Friedman & Lemon, 1989; Meredith, Zackin, Frontera, & Evans, 1989; Tarnopolsky et al., 1988). Increased protein requirements for individuals engaging in resistive activities might be expected due to the need for "extra" dietary protein to synthesize new muscle or repair muscle damage. On the other hand, endurance exercise is associated with marked increases in leucine oxidation (McKenzie et al., 2000; Phillips, Atkinson, Tarnopolsky, & MacDougall, 1993), which would elevate overall requirements for protein (if other amino acids are also oxidized to an appreciable extent), or at least for leucine. The shortcomings of nitrogen balance have long been recognized, as the adequate protein intake is calculated from implausibly high retentions of nitrogen at high protein intakes (Hegsted, 1976; Young, 1986; Young, Gucalp, Rand, Matthews, & Bier, 1987). This highlights the need for another approach to examining protein requirements; tracer-derived estimations of protein requirements are one alternative method. Using this approach, it was reported that consumption of a "low" protein diet (0.86 g $\cdot$ kg^{-1} $\cdot$ day^{-1}) by a group of strength-trained athletes resulted in an accommodated state in which whole body protein synthesis was reduced compared with medium (1.4 g $\cdot$ kg^{-1} $\cdot$ day^{-1}) and high (2.4 g $\cdot$ kg^{-1} $\cdot$ day^{-1}) protein diets (Tarnopolsky et al., 1992). No difference was seen in whole body protein synthesis between the medium and high protein diets, but amino acid oxidation was elevated on the high protein diet, indicating that this protein intake was providing amino acids in excess of the rate at which they could be integrated into body proteins. It should be emphasized that these results do not mean that 1.4 g $\cdot$ kg^{-1} $\cdot$ day^{-1} was required to cover dietary protein needs, but simply that 0.86 g $\cdot$ kg^{-1} $\cdot$ day^{-1} was not sufficient to allow maximal rates of protein synthesis. It is not known what body proteins were being made at a sub-maximal rate at 0.86 g $\cdot$ kg^{-1} $\cdot$ day^{-1}, but if muscle protein synthesis was adversely affected then clearly these data would be of relevance to athletes.

A protein dose–response relationship was shown to exist following resistance exercise (Moore et al., 2009a). In this study, isolated egg protein was fed to young men in graded doses from 0 to 40 g after resistance exercise and MPS was measured. Muscle protein synthesis showed a graded increase from 0 to 20 g and despite doubling protein intake to 40 g, there was no difference in MPS. At the same time that the plateau in MPS was observed, the oxidation of leucine was significantly elevated over that seen at rest and following doses of 5 g and 10 g of protein. The conclusion from these data was that an intake of protein of $\sim$20 g in larger men (85 kg) was sufficient to maximally stimulate MPS, but that higher intakes would not offer any further benefit and the excess amino acids were oxidized (Moore et al., 2009a). Interestingly, the dose of essential amino acids (EAA) in 20 g of egg protein (i.e. 8.3 g) that was found to maximally stimulate MPS was remarkably similar to that seen at rest, which was 10 g of EAA (Cuthbertson et al., 2005). These data (Moore et al., 2009a) suggest that an optimum quantity of protein to consume to maximally stimulate MPS after resistance exercise appears to be around 20–25 g of high-quality protein.

Recent data from Harber and colleagues (2010) suggest that feeding (a drink at 5 kcal $\cdot$ kg^{-1}, which delivered for every 5 kcal: 0.83 g carbohydrate, 0.37 g protein, and 0.03 g fat) did not enhance mixed MPS after a 1 h cycle ride at $\sim$72% of peak oxygen uptake; however, changes in mixed MPS may not capture the feeding-induced enhancement of mitochondrial protein synthesis. Thus, at this time a similar conclusion to that reached by Moore and colleagues on a maximally effective dose of protein is not available for those engaging in endurance exercise, but it would be prudent to measure not only mixed MPS but mitochondrial protein synthesis to isolate the potential effects of the exercise bout on that fraction.

Timing of protein consumption

Athletes have the choice of consuming protein before, during, and after exercise. There are different theories as to which period promotes an optimum adaptation, but in the case of resistance exercise almost all of them relate to the ability of protein to provide amino acid precursors to either support MPS or inhibit MPB. Protein consumption with respect to aerobic exercise focusing on peri-workout/event nutrition is backed by a theory that amino acids could support some energy-yielding pathways and/or attenuate muscle damage and enhance performance. Post-exercise protein consumption may enhance adaptation by also restoring glycogen, but it appears that this is the case only if inadequate carbohydrate is consumed (Jentjens, van Loon, Mann, Wagenmakers, & Jeukendrup, 2001) and this phenomenon will not be discussed here.

With respect to resistance exercise, some studies have shown that pre-exercise protein consumption can enhance MPS (Tipton et al., 2001) and others have shown no effect (Fujita et al., 2009; Tipton et al., 2006). Thus, at this time pre-exercise feeding appears unlikely to increase MPS and long-term gains in muscle mass. A number of training studies have used a combination of pre-exercise and post-exercise feeding to enhance gains in muscle mass (Burk, Timpmann, Medijainen, Vahi, & Oopik, 2009; Cribb & Hayes, 2006), so it is impossible to tell whether the pre-exercise meal imparted any benefit, since post-exercise meals are unequivocally beneficial (see below).

Consumption of protein during exercise may provide amino acids to "prime the pump". In other words, the amino acids present in the circulation during exercise may increase MPS and possibly suppress MPB to enhance protein balance either during or after the exercise bout. Only one study has examined peri-workout protein consumption with resistance exercise (Beelen et al., 2008). In this study, the ingestion of protein and carbohydrate did enhance MPS during the exercise bout and into early recovery, but this did not extend into the overnight fasted period.

A number of studies have provided endurance-trained athletes with protein during a workout to assess the impact of this macronutrient on metabolism and also on performance. Consumption of protein during endurance exercise results in an improved whole body protein balance during and after the exercise bout (Koopman et al., 2004), but the effects on MPS and MPB are not known. Some studies have shown that protein provision during exercise can enhance performance (Saunders et al., 2009; Valentine et al., 2008), but others have shown no performance effect (Cermak et al., 2009; van Essen & Gibala, 2006). Thus, there seems to be little reason to recommend the ingestion of protein during aerobic exercise for performance enhancement and there is no discernible benefit in terms of MPS or MPB.

It is axiomatic that provision of protein and/or amino acids to athletes in the post-exercise period, particularly after resistance exercise, stimulates MPS (for reviews, see Burd et al., 2009; Drummond, Dreyer, Fry, Glynn, & Rasmussen, 2009; Koopman, Saris, Wagenmakers, & van Loon, 2007b; Phillips, Tang, & Moore, 2009). As might be expected, the impact of resistance exercise is quite specific for synthesis of proteins in the myofibrillar protein fraction (Moore et al., 2009b). There are also reports that provision of protein after the performance of aerobic exercise stimulates MPS (Howarth, Moreau, Phillips, & Gibala, 2009; Levenhagen et al., 2001), particularly of the mitochondrial protein fraction (Wilkinson et al., 2008). While there is some debate about the "critical" nature of the timing of post-exercise protein consumption, a simple message may be that the earlier after exercise an athlete consumes protein the better. This conclusion may seem to gloss over a number of important studies showing, or not showing, the benefit of early post-exercise protein provision with respect to both stimulation of MPS and/or hypertrophy, but it emphasizes a principle that athletes would likely benefit from. That is, the sooner the recovery process following exercise can begin the better. So while a crucial "window of anabolic opportunity" is not, at least currently, well defined, it would make sense that protein provision should begin as soon as possible after exercise to promote recovery and possibly to enhance the rate of – or absolute level of – adaptation.

Protein source and quality

Protein quality is measured using a variety of indices but the most commonly accepted and understood index is the protein digestibility corrected amino acid score or PDCAAS. Using the PDCAAS, a number of proteins are classified as "high quality", meaning they have a PDCAAS score of 1.0 or are very close to 1.0. Unsurprisingly, animal-source proteins such as milk (and the constituent proteins of milk, casein and whey), egg, and most meats are high quality. Isolated soy protein, once the anti-nutritional components are removed, also has a PDCAAS score of 1.0. Use of the PDCAAS has been criticized, however, since scores are artificially truncated at 1.0 despite the fact that isolated milk proteins, casein, and whey proteins all have scores of $\sim$1.2 (Phillips et al., 2009; Schaafsma, 2005). An obvious question, therefore, is whether there are any advantages to habitual consumption of these proteins in terms of promotion of recovery (increments in MPS and/or suppression of MPB or less muscle damage) and adaptation (greater muscle mass accretion or enhancement of oxidative capacity). In fact, evidence does exist to support the former thesis that milk proteins, for example, result in a greater stimulation of MPS after resistance exercise than the consumption of equivalent protein and macronutrient energy as isolated soy protein (Wilkinson et al., 2007). Practised over time, the habitual consumption of milk versus equivalent soy protein resulted in greater hypertrophy (Hartman et al., 2007). In addition, comparisons of the capacity of isonitrogenous quantities of soy, casein, and whey protein to stimulate MPS both at rest and following resistance exercise demonstrated the advantage of whey protein (Tang, Moore, Kujbida, Tarnopolsky, & Phillips, 2009). The reasons for the superiority of milk proteins over an ostensibly nutritionally equivalent protein such as isolated soy are not clear, but it appears that the amino acid leucine, possibly in conjunction with the other branched-chain amino acids (BCAA), could be critically important.

Leucine is a BCAA that can activate key signalling proteins resident in the protein kinase B-mammalian target of rapamycin (mTOR) pathway responsible for translation initiation. The effects of leucine have been shown *in vitro* (Atherton, Smith, Etheridge, Rankin, & Rennie, 2010) and *in vivo* (for reviews, see Drummond & Rasmussen, 2008; Drummond et al., 2009; Kimball & Jefferson, 2006a, 2006b). Milk proteins in particular are rich in leucine and this may explain part of their efficacy in stimulating MPS and promoting hypertrophy. Whey protein in particular is highly enriched in leucine, which appears to translate into a greater ability of this protein fraction to stimulate muscle growth, at least compared with soy (Phillips et al., 2009). However, if leucine content is such a significant factor in stimulating MPS, this does not explain the finding that whey protein was more effective than soy, which were both more effective than casein in stimulating MPS following resistance exercise when the leucine contents range from whey with the highest to soy with the lowest (Tang et al., 2009). A critically important observation in this study was the rate of appearance of leucine in the systemic circulation, which was most rapid following whey protein consumption, intermediate with soy protein, and very slow with casein (Tang et al., 2009). Thus, even though casein's leucine content is higher than that of soy, the digestion of casein, which clots in the stomach and so is slowly digested, slowed the appearance of leucine and prevented systemic leucine concentrations from increasing to a sufficient level to turn on MPS. This "leucine trigger" hypothesis for MPS is supported by other observations (Fouillet, Mariotti, Gaudichon, Bos, & Tome, 2002; Lacroix et al., 2006). Interestingly, Koopman and colleagues (2009) reported that partially hydrolysed casein protein improved the rate of MPS post-consumption versus the intact protein. Hydrolysis of casein in this case would allow a more rapid digestion and absorption of the protein and thus a more rapid leucinaemia and a more rapid overall aminoacidaemia, leading to enhanced MPS (Koopman et al., 2009). Thus, a higher leucine content and rapidly digested proteins may be a prudent choice for athletes to consume as the spike in blood leucine appears to be critically important in activating MPS. Sustaining MPS after the initial leucine-mediated activation may well be dependent on adequate provision of the other EAA and in particular the BCAA, which means that supplements of isolated leucine would likely be of little benefit over and above consumption of high-quality proteins, at least for athletes.

Changes in body composition with nutrition and exercise

The key variable determining weight loss is the relative energy deficit created by dietary energy restriction and/or increased energy expenditure. For athletes in particular, weight loss is often a desired goal, but an important question is whether certain patterns of macronutrient consumption can bring about a better "quality" of weight loss. In this sense, the quality of weight loss refers to loss of weight with the highest possible fat-to-lean ratio. In most situations, loss of inert mass as fat is the desired goal of athletes. However, it may be that on occasion an athlete needs to simply lose weight to make a particular weight class for example, and in this scenario it is clear that loss of lean mass would be a "sacrifice" that some athletes may be willing to make. It is also worth noting that a certain amount of skeletal muscle could be lost without much, or any, adverse affect on performance (Degoutte et al., 2006; Zachwieja et al., 2001), but this appears to depend on the rate of weight loss (Garthe, Raastad, Refsnes, Koivisto, & Sundgot-Borgen, 2011). Assuming, however, that fat mass reduction is what most athletes would desire during a period of weight loss with the realization that leanness can offer a competitive advantage, the question is whether there are optimal ratios of nutrients to consume to achieve this goal and also avoid nutritional deprivation.

The macronutrient composition of energy-restricted diets and the influence of these ratios on weight loss is controversial. Many popular weight-loss diets have set protein at $\sim$15% of energy, $<$30% lipids, and $\sim$50–55% carbohydrates, with reductions in dietary fat and increases in dietary fibre being favoured. It is reasonable to reduce energy density with this ratio of macronutrients and promote weight loss in the short term, but low satiety and poor adherence over longer periods are common in people adhering to a diet with this ratio of macronutrients (Abete, Astrup, Martinez, Thorsdottir, & Zulet, 2010; Foreyt et al., 2009; Sacks et al., 2009). Generally speaking, on this diet the tissue composition of weight loss is 70–80% adipose and 20–30% lean tissue (almost exclusively skeletal muscle) (Weinheimer, Sands, & Campbell, 2010). Emerging evidence suggests that reducing the intake of dietary carbohydrates is a critically important step in promoting both greater weight loss and greater loss of body fat (Abete et al., 2010; Foreyt et al., 2009; Krieger, Sitren, Daniels, & Langkamp-Henken, 2006). The mechanisms underpinning this effect are uncertain but may relate to a lower daily blood glucose concentration and also lower daily insulin (Feinman & Fine, 2007). Insulin's primary functions as a hormone are to promote storage of blood glucose in skeletal muscle and adipose tissue and to inhibit lipolysis and promote triglyceride synthesis and storage rather than release (Feinman & Fine, 2007). Another proven strategy is to reduce not just the total quantity of carbohydrate but also to globally lower the glycaemic load of the diet by selecting low glycaemic-index (GI) carbohydrate sources (for a review, see Abete et al., 2010). However, following low carbohydrate, lower GI diets may be a problem for endurance athletes seeking to compete, since dietary carbohydrate intakes are recommended to be higher to allow a more rapid and full recovery of endogenous glycogen stores (Phillips, 2006). Thus, at the expense of carbohydrates, a higher protein or fat intake can obviously compromise performance. While lower total and relative carbohydrate diets appear effective, an important question is what macronutrient should replace the carbohydrate. Diets moderately high in protein and modestly restricted in carbohydrate and fat may have more beneficial effects on body weight homeostasis and associated metabolic variables (Abete et al., 2010; Feinman & Fine, 2007; Foreyt et al., 2009; Krieger et al., 2006; Layman, 2004). This review is aimed at rather moderate protein diets, but still almost twice that recommended by the RDA or RDI (20–30% energy or intakes of 1.8–2.7 g protein $\cdot$ kg^{-1} $\cdot$ day^{-1}, at the expense of carbohydrates), and those with lower carbohydrates (within 40% energy or 3.6 g carbohydrate $\cdot$ kg^{-1} $\cdot$ day^{-1}).

Increasing dietary protein intake to values higher than commonly recommended has a beneficial effect on retention of lean mass during hypoenergetic periods of weight loss (Abete et al., 2010; Feinman & Fine, 2007; Foreyt et al., 2009; Krieger et al., 2006; Layman, 2004). Meta-analyses of trials (Krieger et al., 2006) have shown that higher protein, at the expense of carbohydrate, improves the amount of fat loss and preserves lean tissue. Importantly for athletes, the weight loss-induced decrement in lean mass can be offset by performance of resistive exercise (Layman et al., 2005; MacKenzie, Hamilton, Murray, Taylor, & Baar, 2009; Mettler, Mitchell, & Tipton, 2010). Several studies have shown a synergism between resistance exercise and higher protein content of the diet in terms of enhancing the retention of lean mass during hypoenergetic periods (Layman et al., 2005; MacKenzie et al., 2009; Mettler et al., 2010). Other mechanisms that have been proposed for why protein is an effective substitution for dietary carbohydrate have to do with protein's satiety-promoting effects, which appear to be greater than those of carbohydrate and fat. A comprehensive review of satiety and weight loss is not possible, however. In addition, the thermogenic effect of protein consumption has long been known to be the greatest of all macronutrients.

Other nutrients

The addition of other nutrients to protein may enhance the metabolic effectiveness of protein in either stimulating MPS or suppressing MPB. An important point is that resistance-trained athletes may be less concerned about restoration of muscle glycogen as a goal as opposed to endurance-trained athletes. Nonetheless, an important question, even for resistance-trained athletes, is whether carbohydrate, through insulin, mediates a greater rise in MPS or suppression of MPB, To date three studies have addressed this question and none found that the addition of smaller (20–40 g) or larger (90–120 g) amounts of carbohydrate resulted in enhanced rates of MPS or, at least from whole body measures, suppression of MPB (Glynn et al., 2010; Koopman et al., 2007a). Even when twice as much carbohydrate (50 g as maltodextrin) is added to a sufficient quantity of protein (25 g of whey) there is no further stimulation of MPS or suppression of MPB. Collectively, these findings indicate that so long as protein intake is sufficient, carbohydrate does little to augment post-exercise protein turnover (Glynn et al., 2010; Koopman et al., 2007; Sancak et al., 2010). When viewed from a broad perspective, athletes recovering from exercise would have to serve four "masters": hydration, restoration of metabolized carbohydrate, restoration/repair of damaged proteins, and remodelling proteins. Viewed in this light, protein consumed in a liquid form concurrently with carbohydrate would provide an optimum "package" of nutrients to achieve these goals. Bovine fluid milk would likely represent such a package of nutrients and when consumed as a post-exercise "recovery" drink has been shown to augment lean mass gain (for a review, see Phillips et al., 2009). As far as rehydration is concerned, milk has also been shown to be equivalent or better than water and isotonic sports drinks in terms of restoring fluid balance (Shirreffs, Watson, & Maughan, 2007; Watson, Love, Maughan, & Shirreffs, 2008). A number of studies have also shown that when consumed after exercise, flavoured versions of milk (e.g. chocolate), which most often contain added carbohydrate as a simple sugar, can enhance subsequent exercise performance (Karp et al., 2006; Thomas, Morris, & Stevenson, 2009) and reduce indices of muscle damage (Gilson et al., 2010). It appears that milk, and its flavoured varieties, would be an entirely reasonable and cost-effective alternative to supplements to enhance recovery and enhance performance.

Summary

- Protein consumption can enhance rates of MPS and possibly lower rates of MPB, thus improving muscle NPB. The improvement in NPB appears to accumulate to promote greater protein retention in the case of resistance exercise and may enhance training-induced adaptations with endurance training, although the latter has yet to be tested.
- A dose of protein that appears to maximally stimulate MPS appears to be in the range of 20–25 g, although this estimate may be lower for lighter athletes (i.e. <85 kg).
- Protein may act as more than simply substrate to supply the building blocks for protein synthesis and may be an important trigger to affect phenotypic changes induced by exercise. Leucine in particular occupies a prominent position and may well be critical in enhancing protein-mediated recovery and adaptation as detailed above.
- The rate of digestion of purportedly nutritionally equivalent proteins affects the response of MPS and this appears to be linked to the amplitude and the rate of rise in blood leucine to activate key signalling proteins and turn on MPS.
- The optimum timing for protein ingestion to promote the most favourable recovery and adaptation is after exercise. While data do not yet exist to define exactly how long a theoretical "window of anabolic opportunity" exists, it is safest to state that athletes who are interested in performance need to consume protein as soon as possible after exercise.
- To optimize the ratio of fat-to-lean tissue mass loss during hypoenergetic periods, athletes are advised to ensure that they lower their carbohydrate intake to $\sim 40\%$ of their energy intake (with an emphasis on consumption of lower GI carbohydrates), which usually means no more than 3–4 $g \cdot kg^{-1} \cdot day^{-1}$, and increase their protein intake to ~ 20–30% of their energy intake or ~ 1.8–2.7 $g \cdot kg^{-1} \cdot day^{-1}$. Consideration of how low carbohydrate intake should go would be dictated by how much exercise performance may be compromised by consuming lower than recommended carbohydrates. By engaging in resistance exercise during a hypoenergetic dieting period, athletes will also provide a markedly anabolic stimulus to retain muscle protein. All of the aforementioned strategies will, however, result in less absolute weight loss than if protein is not increased and resistive exercise is not performed, which may be important for some athletes.
- There appears to be no evidence to recommend the addition of carbohydrate to protein sources to optimize the anabolic environment for MPS. For endurance-trained athletes, the same recommendation will quite likely enhance the restoration of glycogen, which may be an important consideration.
- An economical, practical, and efficacious beverage for athletes to consume after exercise is milk, particularly flavoured milk that contains added simple sugar. For the athlete who suffers from lactose maldigestion, there are a number of practical options such as pre-treated lactose reduced milk. This beverage provides fluid that is better retained than water and isotonic sport drinks, carbohydrate to restore muscle glycogen, and high-quality proteins to repair and facilitate adaptive changes in protein synthesis.

References

Abete, I., Astrup, A., Martinez, J. A., Thorsdottir, I., & Zulet, M. A. (2010). Obesity and the metabolic syndrome: Role of different dietary macronutrient distribution patterns and specific nutritional components on weight loss and maintenance. *Nutrition Reviews*, *68*, 214–231.

Atherton, P. J., Smith, K., Etheridge, T., Rankin, D., & Rennie, M. J. (2010). Distinct anabolic signalling responses to amino acids in C2C12 skeletal muscle cells. *Amino Acids*, *38*, 1533–1539.

Beelen, M., Tieland, M., Gijsen, A. P., Vandereyt, H., Kies, A. K., Kuipers, H. et al. (2008). Coingestion of carbohydrate and protein hydrolysate stimulates muscle protein synthesis during exercise in young men, with no further increase during subsequent overnight recovery. *Journal of Nutrition*, *138*, 2198–2204.

Burd, N. A., Tang, J.E., Moore, D. R., & Phillips, S. M. (2009). Exercise training and protein metabolism: Influences of contraction, protein intake, and sex-based differences. *Journal of Applied Physiology*, *106*, 1692–1701.

Burk, A., Timpmann, S., Medijainen, L., Vahi, M., & Oopik, V. (2009). Time-divided ingestion pattern of casein-based protein supplement stimulates an increase in fat-free body mass during resistance training in young untrained men. *Nutrition Research*, *29*, 405–413.

Cermak, N. M., Solheim, A. S., Gardner, M. S., Tarnopolsky, M. A., & Gibala, M. J. (2009). Muscle metabolism during exercise with carbohydrate or protein-carbohydrate ingestion. *Medicine and Science in Sports and Exercise*, *41*, 2158–2164.

Cockburn, E., Stevenson, E., Hayes, P. R., Robson-Ansley, P., & Howatson, G. (2010). Effect of milk-based carbohydrate-protein supplement timing on the attenuation of exercise-induced muscle damage. *Applied Physiology, Nutrition and Metabolism*, *35*, 270–277.

Cribb, P. J., & Hayes, A. (2006). Effects of supplement timing and resistance exercise on skeletal muscle hypertrophy. *Medicine and Science in Sports and Exercise*, *38*, 1918–1925.

Cuthbertson, D., Smith, K., Babraj, J., Leese, G., Waddell, T., Atherton, P. et al. (2005). Anabolic signaling deficits underlie amino acid resistance of wasting, aging muscle. *FASEB Journal*, *19*, 422–424.

Degoutte, F., Jouanel, P., Begue, R. J., Colombier, M., Lac, G., Pequignot, J. M. et al. (2006). Food restriction, performance, biochemical, psychological, and endocrine changes in judo athletes. *International Journal of Sports Medicine*, *27*, 9–18.

Drummond, M. J., Dreyer, H. C., Fry, C. S., Glynn, E. L., & Rasmussen, B. B. (2009). Nutritional and contractile regulation of human skeletal muscle protein synthesis and mTORC1 signaling. *Journal of Applied Physiology*, *106*, 1374–1384.

Drummond, M. J., & Rasmussen, B. B. (2008). Leucine-enriched nutrients and the regulation of mammalian target of rapamycin signalling and human skeletal muscle protein synthesis. *Current Opinion in Clinical Nutrition and Metabolic Care*, *11*, 222–226.

Evans, W. J. (1995). What is sarcopenia? *Journals of Gerontology-Series A: Biological Sciences and Medical Sciences*, *50* (Spec. No.), 5–8.

Feinman, R. D., & Fine, E. J. (2007). Nonequilibrium thermodynamics and energy efficiency in weight loss diets. *Theoretical Biology and Medical Modelling*, *4*, 27.

Foreyt, J. P., Salas-Salvado, J., Caballero, B., Bullo, M., Gifford, K. D., Bautista, I. et al. (2009). Weight-reducing diets: Are there any differences? *Nutrition Reviews*, *67* (suppl. 1), S99–S101.

Fouillet, H., Mariotti, F., Gaudichon, C., Bos, C., & Tome, D. (2002). Peripheral and splanchnic metabolism of dietary nitrogen are differently affected by the protein source in humans as assessed by compartmental modeling. *Journal of Nutrition*, *132*, 125–133.

Friedman, J. E., & Lemon, P. W. (1989). Effect of chronic endurance exercise on retention of dietary protein. *International Journal of Sports Medicine*, *10*, 118–123.

Fujita, S., Dreyer, H. C., Drummond, M. J., Glynn, E. L., Volpi, E., & Rasmussen, B. B. (2009). Essential amino acid and carbohydrate ingestion before resistance exercise does not enhance postexercise muscle protein synthesis. *Journal of Applied Phyiology*, *106*, 1730–1739.

Garthe, I., Raastad, T., Refsnes, P. E., Koivisto, A., & Sundgot-Borgen, J. (2011). Effect of two different weight-loss rates on body composition and strength and power-related performance in elite athletes. *International Journal of Sports Nutrition and Exercise Metabolism*, *21*, 97–104.

Gerovasili, V., Stefanidis, K., Vitzilaios, K., Karatzanos, E., Politis, P., Koroneos, A. et al. (2009). Electrical muscle stimulation preserves the muscle mass of critically ill patients: A randomized study. *Critical Care*, *13*, R161.

Gilson, S. F., Saunders, M. J., Moran, C. W., Moore, R. W., Womack, C. J., & Todd, M. K. (2010). Effects of chocolate milk consumption on markers of muscle recovery following soccer training: A randomized cross-over study. *Journal of the International Society of Sports Nutrition*, *7*, 19.

Glynn, E. L., Fry, C. S., Drummond, M. J., Dreyer, H. C., Dhanani, S., Volpi, E. et al. (2010). Muscle protein breakdown has a minor role in the protein anabolic response to essential amino acid and carbohydrate intake following resistance exercise. *American Journal of Physiology: Regulatory, Integrative, and Comparative Physiology*, *299*, R533–R540.

Greer, B. K., Woodard, J. L., White, J. P., Arguello, E. M., & Haymes, E. M. (2007). Branched-chain amino acid supplementation and indicators of muscle damage after endurance exercise. *International Journal of Sports Nutrition and Exercise Metabolism*, *17*, 595–607.

Harber, M. P., Konopka, A. R., Jemiolo, B., Trappe, S. W., Trappe, T. A., & Reidy, P. T. (2010). Muscle protein synthesis and gene expression during recovery from aerobic exercise in the fasted and fed states. *American Journal of Physiology: Regulatory, Integrative, and Comparative Physiology*, *299*, R1254–R1262.

Hartman, J. W., Moore, D. R., & Phillips, S. M. (2006). Resistance training reduces whole-body protein turnover and improves net protein retention in untrained young males. *Applied Physiology, Nutrition and Metabolism*, *31*, 557–564.

Hartman, J. W., Tang, J. E., Wilkinson, S. B., Tarnopolsky, M. A., Lawrence, R. L., Fullerton, A. V. et al. (2007). Consumption of fat-free fluid milk after resistance exercise promotes greater lean mass accretion than does consumption of soy or carbohydrate in young, novice, male weightlifters. *American Journal of Clinical Nutrition*, *86*, 373–381.

Hegsted, D. M. (1976). Balance studies. *Journal of Nutrition*, *106*, 307–311.

Holm, L., Olesen, J. L., Matsumoto, K., Doi, T., Mizuno, M., Alsted, T. J. et al. (2008). Protein-containing nutrient supplementation following strength training enhances the effect on muscle mass, strength, and bone formation in postmenopausal women. *Journal of Applied Physiology*, *105*, 274–281.

Howarth, K. R., Moreau, N. A., Phillips, S. M., & Gibala, M. J. (2009). Coingestion of protein with carbohydrate during recovery from endurance exercise stimulates skeletal muscle protein synthesis in humans. *Journal of Applied Physiology*, *106*, 1394–1402.

Hundal, H. S., & Taylor, P. M. (2009). Amino acid transceptors: Gate keepers of nutrient exchange and regulators of nutrient signaling. *American Journal of Physiology: Endocrinology and Metabolism*, *296*, E603–E613.

Institute of Medicine (2005). *Dietary reference intakes for energy, carbohydrate, fiber, fat, fatty acids, cholesterol, protein, and amino acids.* Washington, DC: National Academies Press.

Jentjens, R. L., van Loon, L. J., Mann, C. H., Wagenmakers, A. J., & Jeukendrup, A. E. (2001). Addition of protein and amino acids to carbohydrates does not enhance postexercise muscle glycogen synthesis. *Journal of Applied Physiology*, *91*, 839–846.

Karp, J. R., Johnston, J. D., Tecklenburg, S., Mickleborough, T. D., Fly, A. D., & Stager, J. M. (2006). Chocolate milk as a post-exercise recovery aid. *International Journal of Sports Nutrition and Exercise Metabolism*, *16*, 78–91.

Kimball, S. R., & Jefferson, L. S. (2006a). New functions for amino acids: Effects on gene transcription and translation. *American Journal of Clinical Nutriton*, *83*, 500S–507S.

Kimball, S. R., & Jefferson, L. S. (2006b). Signaling pathways and molecular mechanisms through which branched-chain amino acids mediate translational control of protein synthesis. *Journal of Nutrition*, *136*, 227S–231S.

Koopman, R., Beelen, M., Stellingwerff, T., Pennings, B., Saris, W. H., Kies, A. K. et al. (2007a). Coingestion of carbohydrate with protein does not further augment postexercise muscle protein synthesis. *American Journal of Physiology: Endocrinology and Metabolism*, *293*, E833–E842.

Koopman, R., Crombach, N., Gijsen, A. P., Walrand, S., Fauquant, J., Kies, A. K. et al. (2009). Ingestion of a protein hydrolysate is accompanied by an accelerated *in vivo* digestion and absorption rate when compared with its intact protein. *American Journal of Clinical Nutrition*, *90*, 106–115.

Koopman, R., Pannemans, D. L., Jeukendrup, A. E., Gijsen, A. P., Senden, J. M., Halliday, D. et al. (2004). Combined ingestion of protein and carbohydrate improves protein balance during ultra-endurance exercise. *American Journal of Physiology: Endocrinology and Metabolism*, *287*, E712–E720.

Koopman, R., Saris, W. H., Wagenmakers, A. J., & van Loon, L. J. (2007b). Nutritional interventions to promote post-exercise muscle protein synthesis. *Sports Medicine*, *37*, 895–906.

Krieger, J. W., Sitren, H. S., Daniels, M. J., & Langkamp-Henken, B. (2006). Effects of variation in protein and carbohydrate intake on body mass and composition during energy restriction: A meta-regression. *American Journal of Clinical Nutrition*, *83*, 260–274.

Lacroix, M., Bos, C., Leonil, J., Airinei, G., Luengo, C., Dare, S. et al. (2006). Compared with casein or total milk protein, digestion of milk soluble proteins is too rapid to sustain the anabolic postprandial amino acid requirement. *American Journal of Clinical Nutrition*, *84*, 1070–1079.

Layman, D. K. (2004). Protein quantity and quality at levels above the RDA improves adult weight loss. *Journal of the American College of Nutrition*, *23*, 631S–636S.

Layman, D. K., Evans, E., Baum, J. I., Seyler, J., Erickson, D. J., & Boileau, R. A. (2005). Dietary protein and exercise have additive effects on body composition during weight loss in adult women. *Journal of Nutrition*, *135*, 1903–1910.

Lemon, P. W., Tarnopolsky, M. A., MacDougall, J. D., & Atkinson, S. A. (1992). Protein requirements and muscle mass/strength changes during intensive training in novice bodybuilders. *Journal of Applied Physiology*, *73*, 767–775.

Levenhagen, D. K., Gresham, J. D., Carlson, M. G., Maron, D. J., Borel, M. J., & Flakoll, P. J. (2001). Postexercise nutrient intake timing in humans is critical to recovery of leg glucose and protein homeostasis. *American Journal of Physiology: Endocrinology and Metabolism*, *280*, E982–E993.

MacKenzie, M. G., Hamilton, D. L., Murray, J. T., Taylor, P. M., & Baar, K. (2009). mVps34 is activated following high-resistance contractions. *Journal of Physiology*, *587*, 253–260.

Mahoney, D. J., & Tarnopolsky, M. A. (2005). Understanding skeletal muscle adaptation to exercise training in humans: Contributions from microarray studies. *Physical Medicine and Rehabilitation Clinics of North America*, *16*, 859–873, vii.

McKenzie, S., Phillips, S. M., Carter, S. L., Lowther, S., Gibala, M. J., & Tarnopolsky, M. A. (2000). Endurance exercise training attenuates leucine oxidation and BCOAD activation during exercise in humans. *American Journal of Physiology: Endocrinology and Metabolism*, *278*, E580–E587.

Meredith, C. N., Zackin, M. J., Frontera, W. R., & Evans, W. J. (1989). Dietary protein requirements and body protein metabolism in endurance-trained men. *Journal of Applied Physiology*, *66*, 2850–2856.

Mettler, S., Mitchell, N., & Tipton, K. D. (2010). Increased protein intake reduces lean body mass loss during weight loss in athletes. *Medicine and Science in Sports and Exercise*, *42*, 326–337.

Moore, D. R., Del Bel, N. C., Nizi, K. I., Hartman, J. W., Tang, J. E., Armstrong, D. et al. (2007). Resistance training reduces fasted- and fed-state leucine turnover and increases dietary nitrogen retention in previously untrained young men. *Journal of Nutrition*, *137*, 985–991.

Moore, D. R., Phillips, S. M., Babraj, J. A., Smith, K., & Rennie, M. J. (2005). Myofibrillar and collagen protein synthesis in human skeletal muscle in young men after maximal shortening and lengthening contractions. *American Journal of Physiology: Endocrinology and Metabolism*, *288*, E1153–E1159.

Moore, D. R., Robinson, M. J., Fry, J. L., Tang, J. E., Glover, E. I., Wilkinson, S. B. et al. (2009a). Ingested protein dose response of muscle and albumin protein synthesis after resistance exercise in young men. *American Journal of Clinical Nutrition*, *89*, 161–168.

Moore, D. R., Tang, J. E., Burd, N. A., Rerecich, T., Tarnopolsky, M. A., & Phillips, S. M. (2009b). Differential stimulation of myofibrillar and sarcoplasmic protein synthesis with protein ingestion at rest and after resistance exercise. *Journal of Physiology*, *597*, 897–904.

Phillips, S. M. (2006). Dietary protein for athletes: From requirements to metabolic advantage. *Applied Physiology, Nutrition and Metabolism*, *31*, 647–654.

Phillips, S. M., Atkinson, S. A., Tarnopolsky, M. A., & MacDougall, J. D. (1993). Gender differences in leucine kinetics and nitrogen balance in endurance athletes. *Journal of Applied Physiology*, *75*, 2134–2141.

Phillips, S. M., Tang, J. E., & Moore, D. R. (2009). The role of milk- and soy-based protein in support of muscle protein synthesis and muscle protein accretion in young and elderly persons. *Journal of the American College of Nutrition*, *28*, 343–354.

Rennie, M. J., Wackerhage, H., Spangenburg, E. E., & Booth, F. W. (2004). Control of the size of the human muscle mass. *Annual Review of Physiology*, *66*, 799–828.

Robinson, M. M., Turner, S. M., Hellerstein, M. K., Hamilton, K. L., & Miller, B. F. (2011).Long-term synthesis rates of skeletal muscle DNA and protein are higher during aerobic training in older humans than in sedentary young subjects but are not altered by protein supplementation. *FASEB Journal* (DOI: 10.1096/fj.11-186437).

Rowlands, D. S., Rossler, K., Thorp, R. M., Graham, D. F., Timmons, B. W., Stannard, S. R. et al. (2008). Effect of dietary protein content during recovery from high-intensity cycling on subsequent performance and markers of stress, inflammation, and muscle damage in well-trained men. *Applied Physiology, Nutrition and Metabolism*, *33*, 39–51.

Rowlands, D. S., Thorp, R. M., Rossler, K., Graham, D. F., & Rockell, M. J. (2007). Effect of protein-rich feeding on recovery after intense exercise. *International Journal of Sport Nutrition and Exercise Metabolism*, *17*, 521–543.

Sacks, F. M., Bray, G. A., Carey, V. J., Smith, S. R., Ryan, D. H., Anton, S. D. et al. (2009). Comparison of weight-loss diets with different compositions of fat, protein, and carbohydrates. *New England Journal of Medicine*, *360*, 859–873.

Sakuma, K., Watanabe, K., Hotta, N., Koike, T., Ishida, K., Katayama, K. et al. (2009). The adaptive responses in several mediators linked with hypertrophy and atrophy of skeletal muscle after lower limb unloading in humans. *Acta Physiologica (Oxford)*, *197*, 151–159.

Sancak, Y., Bar-Peled, L., Zoncu, R., Markhard, A. L., Nada, S., & Sabatini, D. M. (2010). Ragulator-Rag complex targets mTORC1 to the lysosomal surface and is necessary for its activation by amino acids. *Cell*, *141*, 290–303.

Sarbassov, D. D., Ali, S. M., Kim, D. H., Guertin, D. A., Latek, R. R., Erdjument-Bromage, H. et al. (2004). Rictor, a novel binding partner of mTOR, defines a rapamycin-insensitive and raptor-independent pathway that regulates the cytoskeleton. *Current Biology*, *14*, 1296–1302.

Saunders, M. J., Moore, R. W., Kies, A. K., Luden, N. D., & Pratt, C. A. (2009). Carbohydrate and protein hydrolysate coingestions improvement of late-exercise time-trial performance. *International Journal of Sport Nutrition and Exercise Metabolism*, *19*, 136–149.

Schaafsma, G. (2005). The Protein Digestibility-Corrected Amino Acid Score (PDCAAS) – a concept for describing protein quality in foods and food ingredients: A critical review. *Journal of AOAC International*, *88*, 988–994.

Shirreffs, S. M., Watson, P., & Maughan, R. J. (2007). Milk as an effective post-exercise rehydration drink. *British Journal of Nutrition*, *98*, 173–180.

Tang, J. E., Moore, D. R., Kujbida, G. W., Tarnopolsky, M. A., & Phillips, S. M. (2009). Ingestion of whey hydrolysate, casein, or soy protein isolate: Effects on mixed muscle protein synthesis at rest and following resistance exercise in young men. *Journal of Applied Physiology*, *107*, 987–992.

Tarnopolsky, M. A., Atkinson, S. A., MacDougall, J. D., Chesley, A., Phillips, S., & Schwarcz, H. P. (1992). Evaluation of protein requirements for trained strength athletes. *Journal of Applied Physiology*, *73*, 1986–1995.

Tarnopolsky, M. A., MacDougall, J. D., & Atkinson, S. A. (1988). Influence of protein intake and training status on nitrogen balance and lean body mass. *Journal of Applied Physiology*, *64*, 187–193.

Thomas, K., Morris, P., & Stevenson, E. (2009). Improved endurance capacity following chocolate milk consumption compared with two commercially available sport drinks. *Applied Physiology, Nutrition and Metabolism*, *34*, 78–82.

Tipton, K. D., Elliott, T. A., Cree, M. G., Aarsland, A. A., Sanford, A. P., & Wolfe, R. R. (2006). Stimulation of net muscle protein synthesis by whey protein ingestion before and after exercise. *American Journal of Physiology: Endocrinology and Metabolism*, *292*, E71–E76.

Tipton, K. D., Rasmussen, B. B., Miller, S. L., Wolf, S. E., Owens-Stovall, S. K., Petrini, B. E. et al. (2001). Timing of amino acid-carbohydrate ingestion alters anabolic response of muscle to resistance exercise. *American Journal of Physiology: Endocrinology and Metabolism*, *281*, E197–E206.

Valentine, R. J., Saunders, M. J., Todd, M. K., & St. Laurent, T. G. (2008). Influence of carbohydrate-protein beverage on cycling endurance and indices of muscle disruption. *International Journal of Sport Nutrition and Exercise Metabolism*, *18*, 363–378.

Van Essen, M., & Gibala, M. J. (2006). Failure of protein to improve time trial performance when added to a sports drink. *Medicine and Science in Sports and Exercise*, *38*, 1476–1483.

Watson, P., Love, T. D., Maughan, R. J., & Shirreffs, S. M. (2008). A comparison of the effects of milk and a carbohydrate-electrolyte drink on the restoration of fluid balance and exercise capacity in a hot, humid environment. *European Journal of Applied Physiology*, *104*, 633–642.

Weinheimer, E. M., Sands, L. P., & Campbell, W. W. (2010). A systematic review of the separate and combined effects of energy restriction and exercise on fat-free mass in middle-aged and older adults: Implications for sarcopenic obesity. *Nutrition Reviews*, *68*, 375–388.

Wilkinson, S. B., Phillips, S. M., Atherton, P. J., Patel, R., Yarasheski, K. E., Tarnopolsky, M. A. et al. (2008). Differential effects of resistance and endurance exercise in the fed state on signalling molecule phosphorylation and protein synthesis in human muscle. *Journal of Physiology*, *586*, 3701–3717.

Wilkinson, S. B., Tarnopolsky, M. A., MacDonald, M. J., Macdonald, J. R., Armstrong, D., & Phillips, S. M. (2007). Consumption of fluid skim milk promotes greater muscle protein accretion following resistance exercise than an isonitrogenous and isoenergetic soy protein beverage. *American Journal of Clinical Nutrition*, *85*, 1031–1040.

Young, V. R. (1986). Nutritional balance studies: Indicators of human requirements or of adaptive mechanisms? *Journal of Nutrition*, *116*, 700–703.

Young, V. R., Gucalp, C., Rand, W. M., Matthews, D. E., & Bier, D. M. (1987). Leucine kinetics during three weeks at submaintenance-to-maintenance intakes of leucine in men: Adaptation and accommodation. *Human Nutrition Clinical Nutrition*, *41*, 1–18.

Zachwieja, J. J., Ezell, D. M., Cline, A. D., Ricketts, J. C., Vicknair, P. C., Schorle, S. M. et al. (2001). Short-term dietary energy restriction reduces lean body mass but not performance in physically active men and women. *International Journal of Sports Nutrition*, *22*, 310–316.