

# Facts From Feces: Nitrogen Still Measures Up as a Nutritional Index for Mammalian Herbivores

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**ABSTRACT** Fecal nitrogen (FN) has been applied widely as an index of dietary quality in studies of nutritional ecology of free-ranging and captive vertebrate herbivores, particularly ruminants. Three related articles in the *Journal of Wildlife Management* (*JWM*; Leslie and Starkey 1985, 1987; Hobbs 1987) have been cited ( $n = 150$ ) in 87 publications and 39 peer-reviewed journals. The critique by Hobbs (1987) and the reply by Leslie and Starkey (1987) on limitations and appropriate applications of FN have been used to justify use of FN or negate its value as a nutritional proxy. We undertook a retrospective analysis of FN applications since 1985, largely because we sensed that methodological cautions noted in the 3 *JWM* publications were not being followed, leading to faulty conclusions and management applications, and that application protocols needed updating. From January 1986 through July 2007, the 107 species-by-continent applications of FN, citing the 3 *JWM* publications singly or in any combination, were diverse; FN was used in various ways on 5 continents and for 50 wild and domestic species. Cumulative rates of departure from recommended FN applications increased in recent years, largely in studies that compare different species while failing to fully acknowledge that differences likely reflected digestive capabilities rather than differences in some aspect of dietary intake. Post-1985 research on plant secondary compounds (e.g., tannins) has refined limitations to the application of FN, permitting more straightforward protocols than were possible in 1985. Although use does not necessarily reflect value, the number of published applications during the past 22 years indicates that peer reviewers from a variety of scientific disciplines view FN as a suitable proxy for nutritional status, which can be used to contrast study units when carefully defined by the study design. Any index can have shortcomings, and there are still circumstances when application of FN is problematic. Precise prediction of intake with FN under field conditions is still hampered by inherent variability, but contrasts of comparable study units and species can be appropriate. Published protocols for FN, as amended herein, should be adhered to, and conclusions are strengthened by the use of multiple nutritional indices. (*JOURNAL OF WILDLIFE MANAGEMENT* 72(6):1420–1433; 2008)

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Because studies of nutritional ecology of free-ranging herbivores can be time consuming and expensive to conduct, some investigators used fecal indices (e.g., Putman 1984, Kohn and Wayne 1997) to evaluate relationships of nutrition with diet, demography, and behavior. Animal scientists were among the first to establish relationships of fecal constituents, notably nitrogen (N), with quality and quantity of diets of domestic herbivores (e.g., Kotb and Luckey 1972, Cordova et al. 1978, Holechek et al. 1982). Although some wildlife management treatises advocated use of fecal N (FN; Caughley and Sinclair 2002), others warned of its shortcomings (Robbins 1983, Servello et al. 2005). After evaluating effects of plant secondary compounds (e.g., Freeland and Janzen 1974), specifically tannins, on protein digestion and excretion in 5 ungulate species, Robbins et al. (1987:103) offered what stands as the strongest criticism of FN by concluding that it “is not a precise indicator of any dietary parameter and should not be used in ecological studies.”

Fecal material of many free-ranging herbivores is readily available, making an index based on its components appealing. Under conditions lacking extensive dung beetle activity, as is common in Africa (Wrench et al. 1996), exposure of feces to weather and other insects does not

compromise retention of N for 2–3 weeks postdefecation, making FN a useful index under field applications when relatively fresh feces can be obtained (Jenks et al. 1990, Osborn et al. 2002, Kamler et al. 2003a). Nevertheless, debate over the accuracy and application of FN has not abated.

Following earlier investigations on wild ruminants (e.g., Arman et al. 1975), Leslie and Starkey (1985) demonstrated positive relationships of FN to dietary N, dietary phosphorus, and dietary dry matter digestibility in Roosevelt elk (*Cervus elaphus roosevelti*) and Columbian black-tailed deer (*Odocoileus hemionus columbianus*). Those authors cautioned that applications of FN were constrained by differences in species-specific digestive capabilities, study areas, and study conditions and the potential consequences of consuming plant secondary compounds (Robbins et al. 1987, Dearing et al. 2005). After re-evaluation of data in Sinclair et al. (1982) and Leslie and Starkey (1985), Hobbs (1987) echoed concerns of Robbins et al. (1987) and concluded that FN was not a reliable predictor of dietary quality because of the influence of intra-seasonal and inter-animal variability and plant secondary compounds. Nevertheless, Hobbs (1987:319) also concluded that “specific regressions [could] be useful in specific locations.” Neither Robbins et al. (1987) nor Hobbs (1987) offered any definition of precision. Leslie and Starkey (1987) countered by outlining condi-

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tions, not requiring precise prediction, under which FN provided useful insight on nutritional ecology of free-ranging herbivores.

In 22 years since publication of Leslie and Starkey (1985, 1987) and Hobbs (1987), many applications of FN appeared in wildlife, ecological, and mammalian journals. Those 3 *Journal of Wildlife Management (JWM)* publications were cited to either justify or negate use of FN in nutritional studies of vertebrate herbivores. Until recently, we only informally tracked the number and appropriateness of post-1985 published applications of FN as proxies for dietary quality of free-ranging herbivores and correlates to various aspects of their ecologies. In recent years, however, we became concerned by what seems to be a growing number of misapplications of FN in field-based research.

If research progress on the limitations of FN applications has not been made, it is still appropriate to follow recommendations of Hobbs (1987) and Leslie and Starkey (1987) to avoid misleading conclusions and faulty management recommendations. If, however, research progress has been made, particularly in the area of plant secondary compounds, it is time to reevaluate application protocols for FN. Therefore, we undertook a retrospective analysis of articles published in scientific serials that cited Leslie and Starkey (1985, 1987) and Hobbs (1987) and used FN applications to elucidate some aspect of the nutritional ecology of vertebrate herbivores. We focused on 1) applications that did not appear to adhere to recommendations in the 3 *JWM* publications and 2) research that ameliorated known limitations of the FN technique. We hypothesized that misapplications would become more frequent as length of time from publication of Leslie and Starkey (1985, 1987) and Hobbs (1987) increased because dated literature can be overlooked when authors and editors seek only current literature for comparison or when investigators become satisfied with a methodology as their experience with it increases (i.e., weight-of-evidence approach).

## METHODS

We used Web of Science (Thomson Scientific, Inc., Philadelphia, PA) to locate publications in refereed journals that applied FN as an index of dietary quality and cited Leslie and Starkey (1985, 1987) and Hobbs (1987), singly or in any combination, from January 1986 through July 2007. We also conducted general searches with the key words “fecal nitrogen,” and their variants, using Web of Science, BiblioLine—Wildlife & Ecology Studies Worldwide (NISC International, Baltimore, MD), and Google Scholar (Google Inc., Mountain View, CA). We evaluated other published studies from 1986 onward that used FN but did not cite the 3 *JWM* publications; we did not include theses, dissertations, or published abstracts from professional meetings.

Generally, we used cautions from Hobbs (1987) and criteria of Leslie and Starkey (1987) to judge appropriateness of FN applications. “FN alone represents a viable index

of: (1) relative changes in interseasonal diet quality of a single population (assuming no radical changes in the consumption of secondary compounds), (2) single-season comparisons of a population between years (assuming no radical changes in forage availability and thus dietary selection), and (3) within-season comparisons of disjunct populations that occupy similar habitats and therefore are likely to consume similar diets; i.e., a minimization of differing effects of secondary plant metabolites” (Leslie and Starkey 1987:324).

Considerable differences exist in digestive strategies, physiologies, and morphologies of terrestrial herbivores that thereby affect levels of FN (Robbins 1983, Van Soest 1994). We considered studies that made direct or statistical interspecific comparisons inappropriate if they led to conclusions that differences resulted from dietary quality alone. In retrospect, this constraint of FN was not articulated clearly in any of the 3 *JWM* publications, albeit it could be inferred (Leslie and Starkey 1987). Similarly, intraspecific sexual differences in digestive morphology were documented in white-tailed deer (*O. virginianus*; Jenks et al. 1994) and other ruminants (Barboza and Bowyer 2000, 2001), but their influence on the FN–dietary N relationship does not appear problematic. Some studies failed to document sexual differences in FN when females and males of the same species were on similar diets (e.g., impala [*Aepyceros melampus*]; Wrench et al. 1996), but such observations probably were dependent on the degree of sexual size dimorphism by species (i.e., Bowyer 2004).

Current methodological standards for FN applications caution that the FN–dietary N relationship can be compromised if plant secondary compounds elevate FN irrespective of dietary N. High levels of FN may reflect not only high levels of dietary N but also N from various sources (e.g., microbial or dietary) bound to such compounds. Therefore, prevailing concern exists when comparing 2 populations of herbivores from areas with disparate forage availabilities relative to levels of ingested plant secondary compounds (either in a single season or inter-seasonally). Although nutritional differences certainly would exist between the 2 populations if FN was disparate between them, they may not reflect only levels of N consumed. Therefore, we critically evaluated published research on plant secondary compounds relative to FN applications to ascertain if post-1985 insights ameliorate earlier concerns.

We compiled various summary metrics from published applications of FN: journal frequency for published studies, species-by-continent applications, study type, and correlates with FN. We evaluated papers for misapplications of FN and analyzed them through time.

## RESULTS

### Trends in FN Applications

The 3 *JWM* publications were cited 150 times in 87 refereed publications from January 1986 through July 2007: Leslie and Starkey (1985), 66 times; Hobbs (1987), 49 times; Leslie and Starkey (1987), 35 times. Only 3 refereed

**Table 1.** Predominant scientific serials ( $n = 39$ ) in which most of 150 citations of Leslie and Starkey (1985, 1987) and Hobbs (1987) have occurred, January 1986–July 2007.

Scientific serial	n	%	Yr	
			Initial citation	Most recent citation
<i>Journal of Wildlife Management</i>	16	18.4	1987	2003
<i>Journal of Mammalogy</i>	9	10.3	1987	2006
<i>Oecologia</i>	5	5.7	1988	2001
<i>Journal of Range Management</i>	5	5.7	1992	1996
<i>Acta Theriologica</i>	4	4.5	1986	2007
<i>Folia Zoologica</i>	3	3.4	2003	2005
<i>South African Journal of Wildlife Research</i>	3	3.4	1996	2003

publications (Massey et al. 1994, Wrench et al. 1997, Spaeth et al. 2002) that cited  $\geq 1$  of the 3 *JWM* publications were not identified in our Web of Science search; we added them to our summaries. That low omission rate suggested that the Web of Science database was quite robust and failed to include only about 3% of such cross-cited publications, mindful that it did not index all scientific serials (e.g., *Alces*, *Koekoe*, and *Rangifer*).

The 87 publications that cited the 3 *JWM* publications in some combination appeared in 39 peer-reviewed journals and most frequently in *JWM* ( $n = 16$ , 18.4%) and the *Journal of Mammalogy* ( $n = 9$ , 10.3%; Table 1). The remaining 37 outlets represented a variety of disciplines that publish international journals such as *Behaviour*, *Ecology*, *Canadian Journal of Zoology*, *Oecologia*, *Journal of Zoology (London)*, and *Wildlife Biology*. The 3 *JWM* publications were cited in some journals that most wildlife biologists are unlikely to encounter, at least with any regularity: *American Journal of Physical Anthropology*, *Onderstepoort Journal of Veterinary Research*, and *Landbauforschung Völknerode*.

Of the 87 publications, 16 (18.4%) did not report original observations of FN (e.g., review papers such as Kohn and Wayne 1997); 8 (9.2%) used the cautions of Hobbs (1987) to negate use of FN as an index of dietary quality, sometimes opting for another approach (e.g., fecal diaminopemelic acid; Main and Coblenz 1996); 5 (5.7%) provided syntheses and analyses of various indices of dietary quality (Wehausen 1995, Garrott et al. 1996, Kohn and Wayne 1997, Cook et al. 2001, Clark et al. 2003); and 1 (1.1%) used poor correlations of FN to percentages of various forages and forage classes in the diet to conclude that FN was useful to elucidate only broad seasonal trends in dietary quality (Massey et al. 1994).

Since 1986, the 107 species-by-continent applications that cited the 3 *JWM* publications and provided new FN data were diverse; FN was used in various applications on 5 continents and for 50 wild and domestic species (Table 2). The greatest number of applications of FN by species occurred in Africa ( $n = 4$  primates and 22 ungulates), but the greatest number of published studies originated in North America ( $n = 47$ ). Fecal nitrogen was used to study omnivores (e.g., baboons [*Papio* spp.]) and herbivorous birds

(e.g., red grouse [*Lagopus lagopus*]) as well as other mammals. Most applications of FN involved ruminants, but the methodology also was used with hindgut fermenters (e.g., domestic horses and African bush elephants [*Loxodonta africana*]). The greatest number of FN applications were on white-tailed deer, North American elk and red deer (*Cervus elaphus*), and bighorn sheep (*Ovis canadensis*; Table 2).

Through time, cumulative numbers of FN applications relative to the number of publications, journals, species, and species-specific populations grew linearly; about 4 applications were undertaken per year and subsequently published in peer-reviewed literature from January 1986 through July 2007 (Fig. 1A, B). Therefore, the collective citing half-life (no. of yr in which 50% of a paper's total citations occur; Garfield 1994) of the 3 *JWM* publications was high. Research in journals such as *JWM* often has citing half-lives of  $>10$  years (Kokko and Sutherland 1999, Leslie 2007).

Applied field applications with free-ranging species represented 77% of published research, and 23% of the applications were methodological or experimental with captive species or a mix of captive-domestic, hand-led (tame), and free-ranging species. Eight studies were designed specifically with captive or confined herbivores to evaluate predictive relationships of FN and intake of particular nutrients (Loeb and Schwab 1989, Leite and Stuth 1990, Nunez-Hernandez et al. 1992, Irwin et al. 1993, Cook et al. 1994, Hodgman et al. 1996, Wrench et al. 1997, Mésoschina et al. 1998). One recent paper successfully retested reliability of the FN–dietary N relationship (Leslie and Starkey 1985) on free-ranging sika (*Cervus nippon*) in Japan (Ueno et al. 2007). Twenty-six studies reported significant correlations of FN with 38 nutritional, ecological, behavioral, and demographic characteristics in captive and free-ranging populations (Table 3). Of those 26 studies, 10 also identified 21 variables, 13 of which were particular proportions of dietary constituents, that were not correlated with FN (Table 4).

Forty-six (52.8%) of the published studies assumed that FN provided a useful proxy of nutrition or condition and addressed limitations by articulating how they adhered to protocols outlined in the 3 *JWM* publications. Contrasts of FN to various intraspecific characteristics included differences in intersexual diet and habitat use (Beier 1987, Schaefer and Messier 1995, Post et al. 2001, Sakuragi et al. 2003, Mooring et al. 2005), predation risk (Festa-Bianchet 1988, Hernández and Laundré 2005, Hebblewhite et al. 2005), maternal behavior and reproductive patterns (Rachlow and Bowyer 1994, Hass 1997, Rubin et al. 2000, Côté and Festa-Bianchet 2001), activity patterns (Schaefer and Messier 1996), effects of domestic species (Jenks et al. 1996), population density (Sams et al. 1998, Asada and Ochiai 1999, van der Waal et al. 2003, Blanchard et al. 2003, Nicholson et al. 2006, Miyashita et al. 2007), supplemental feeding (Osborn and Jenks 1998, Page and Underwood 2006), and human influences (Rubin et al. 2002, Treydte et al. 2006, Walter et al. 2006).

**Table 2.** Species by continent for which fecal nitrogen<sup>a</sup> values were reported and incorrect species-specific applications relative to recommendations of Leslie and Starkey (1985, 1987) and Hobbs (1987).

Continent and species	No. of applications	No. of incorrect applications	References
<b>Africa</b>			
Primates			
Chacma baboon ( <i>Papio ursinus</i> )	1	1	Codron et al. 2006 <sup>a</sup> <sup>b</sup>
Gelada baboon ( <i>Theropithecus gelada</i> )	1	1	Dunbar and Bose 1991 <sup>b</sup>
Olive baboon ( <i>Papio anubis</i> )	1	1	Dunbar and Bose 1991 <sup>b</sup>
Western gorilla ( <i>Gorilla gorilla</i> )	1	0	Plumptre 1995
Ungulates			
African buffalo ( <i>Syncerus caffer</i> )	4	1	Prins and Beekman 1989; Plumptre 1995; Codron et al. 2006 <sup>b</sup> , <sup>b</sup> 2007
African bush elephant ( <i>Loxodonta africana</i> )	2	1	Plumptre 1995, Codron et al. 2006 <sup>b</sup>
Black-fronted duiker ( <i>Cephalophus nigrifrons</i> )	1	0	Plumptre 1995
Black rhinoceros ( <i>Diceros bicornis</i> )	1	0	Codron et al. 2007
Blue wildebeest ( <i>Connochaetes taurinus</i> )	3	1	Wrench et al. 1997; Codron et al. 2006 <sup>b</sup> , <sup>b</sup> 2007
Burchell's zebra ( <i>Equus burchellii</i> )	5	3	Dunbar and Bose 1991; <sup>b</sup> Wrench et al. 1997; Codron et al. 2006 <sup>a</sup> , <sup>b</sup> <sup>b</sup> , <sup>b</sup> 2007
Bushbuck ( <i>Tragelaphus scriptus</i> )	2	0	Plumptre 1995, Codron et al. 2007
Bush duiker ( <i>Sylvicapra grimmia</i> )	1	0	Codron et al. 2007
Common eland ( <i>Taurotragus oryx</i> )	1	0	Codron et al. 2007
Common hippopotamus ( <i>Hippopotamus amphibius</i> )	1	0	Codron et al. 2007
Common tsessebe ( <i>Damaliscus lunatus</i> )	1	0	Codron et al. 2007
Common warthog ( <i>Phacochoerus africanus</i> )	2	0	Treydte et al. 2006, Codron et al. 2007
Giraffe ( <i>Giraffa camelopardalis</i> )	3	2	Codron et al. 2006 <sup>a</sup> , <sup>b</sup> <sup>b</sup> , <sup>b</sup> 2007
Greater kudu ( <i>Tragelaphus strepsiceros</i> )	3	1	van der Waal et al. 2003; Codron et al. 2006 <sup>b</sup> , <sup>b</sup> 2007
Impala ( <i>Aepyceros melampus</i> )	4	2	Wrench et al. 1997, Codron et al. 2006 <sup>a</sup> , <sup>b</sup> <sup>b</sup> , <sup>b</sup> 2007
Nyala ( <i>Tragelaphus angasii</i> )	1	0	Codron et al. 2007
Roan antelope ( <i>Hippotragus equinus</i> )	1	0	Codron et al. 2007
Sable antelope ( <i>Hippotragus niger</i> )	1	0	Codron et al. 2007
Steenbok ( <i>Raphicerus campestris</i> )	1	0	Codron et al. 2007
Waterbuck ( <i>Kobus ellipsiprymnus</i> )	1	0	Codron et al. 2007
White rhinoceros ( <i>Ceratotherium simum</i> )	1	0	Codron et al. 2007
Domestic cattle	3	1	Dunbar and Bose 1991, <sup>b</sup> Grant et al. 1996 <sup>b</sup> , Wrench et al. 1997
<b>Asia</b>			
Alpine musk deer ( <i>Moschus chrysogaster</i> )	1	0	Green 1987
Blackbuck ( <i>Antelope cervicapra</i> )	1	0	Jhala 1997
Mongolian gazelle ( <i>Procapra gutturosa</i> )	1	0	Jiang et al. 2002
Reeves' muntjacs ( <i>Muntiacus reevesi</i> )	1	0	McCullough et al. 2000
Sika ( <i>Cervus nippon</i> )	5	0	Asada and Ochiai 1999, Sakuragi et al. 2003, Jiang et al. 2005, Miyashita et al. 2007, Ueno et al. 2007
<b>Europe</b>			
European roe ( <i>Capreolus capreolus</i> )	3	2	Wahlström and Kjellander 1995, Kamler et al. 2004, <sup>b</sup> Kamler and Homolka 2005 <sup>b</sup>
Red deer ( <i>Cervus elaphus</i> )	4	2	Kamler et al. 2003 <sup>a</sup> , <sup>b</sup> , 2004; <sup>b</sup> Kamler and Homolka 2005 <sup>b</sup>
Red grouse ( <i>Lagopus lagopus</i> )	1	0	Moss et al. 1990
Domestic cattle	1	0	Schmidt et al. 1999
Domestic horse	1	0	Mésoschina et al. 1998
Domestic sheep	1	0	Schmidt et al. 1999
<b>South America</b>			
Plains vizcacha ( <i>Lagostomus maximus</i> )	1	0	Branch et al. 1994
<b>North America</b>			
American bison ( <i>Bison bison</i> )	3	0	Post et al. 2001, Hernández and Laundré 2005, Mooring et al. 2005
Bighorn sheep ( <i>Ovis canadensis</i> )	8 <sup>b</sup>	0	Festa-Bianchet 1988; Irwin et al. 1993; <sup>c</sup> Hass 1997; Rubin et al. 2000, 2002; Blanchard et al. 2003; Oehler et al. 2003; McKinney et al. 2006
Dall's sheep ( <i>Ovis dalli</i> )	1	0	Rachlow and Bowyer 1994
North American elk ( <i>Cervus elaphus</i> )	5	0	Cook et al. 1994, Gogan and Barrett 1995, Hebblewhite et al. 2005, Hernández and Laundré 2005, Walter et al. 2006
Caribou ( <i>Ranifer tarandus</i> )	1	0	Ferguson et al. 1988
Moose ( <i>Alces alces</i> )	1	0	Leslie et al. 1989
Mountain goat ( <i>Oreamnos americanus</i> )	1	0	Côté and Festa-Bianchet 2001

Table 2. Continued.

Continent and species	No. of applications	No. of incorrect applications	References
Mule deer ( <i>Odocoileus hemionus</i> )	6	0	Robbins et al. 1987, Massey et al. 1994, Gogan and Barrett 1995, Hodgman et al. 1996, <sup>d</sup> Kucera 1997, Nicholson et al. 2006
Muskox ( <i>Ovibos moschatus</i> )	2	0	Schaefer and Messier 1995, 1996
Pocket gopher ( <i>Thomomys bottae</i> )	1	0	Loeb and Schwab 1989
Pronghorn ( <i>Antilocapra americana</i> )	1	0	Dunbar et al. 1999
White-tailed deer ( <i>Odocoileus virginianus</i> )	14	0	Hodgman and Bowyer 1986, Beier 1987, Robbins et al. 1987, Jenks et al. 1989, Leslie et al. 1989, Howery and Pfister 1990, Ruthven et al. 1994, Brown et al. 1995, Jenks et al. 1996, Osborn and Jenks 1998, Sams et al. 1998, Osborn and Ginnett 2001, Osborn et al. 2002, Page and Underwood 2006
Domestic cattle	4	0	Leite and Stuth 1990, Nunez-Hernandez et al. 1992, Pitts et al. 1992, Jenks et al. 1996
Domestic goat	1	0	Nunez-Hernandez et al. 1992
Total	107	19	

<sup>a</sup> Sixteen publications cited the 3 *JWM* publications but did not report any new FN data: Molvar et al. 1993, Pietersen et al. 1993, Holand 1994, Wehausen 1995, Garrott et al. 1996, Grant et al. 1996a, Jiang and Hudson 1996, Main and Coblenz 1996, Meissner and Pieterse 1996, Kohn and Wayne 1997, Cook et al. 2001, Dennehy 2001, Spaeth et al. 2002, Clark et al. 2003, Mooring et al. 2003, Li et al. 2004.

<sup>b</sup> Incorrect application.

<sup>c</sup> Study also included captive bighorn-mouflon (*Ovis orientalis*) crosses.

<sup>d</sup> We tallied this study twice because it included 2 subspecies: *O. b. hemionus* and *O. b. columbianus*.

Post-1985 articles that used or evaluated FN but did not cite the 3 *JWM* publications included the following. The Grazing Land Technology Institute of the Natural Resources Conservation Service used FN from near infrared reflectance spectroscopy (vs. more expensive traditional wet chemistry techniques; cf. Kamler et al. 2004) in their nationwide monitoring program to assess dietary crude protein and digestible organic matter from feces of domestic cattle (United States Department of Agriculture 2000). Other applications of FN involved domestic (Chenost 1985, de Alba Becerra et al. 1998, Lukas et al. 2005) and wild species, including voles (*Microtus pennsylvanicus*; Bergeron 1996), North American elk (Morgantini and Hudson 1989), sambar deer (*Cervus unicolor*; Padmalal et al. 2003), Pyrenean chamois (*Rupicapra pyrenaica*; Dalmau et al. 2007), bighorn sheep (Bleich et al. 1997), Asiatic wild ass (*Equus hemionus*), Dorcas gazelles (*Gazella dorcas*; Henley and Ward 2006), other African ruminants (Grant et al. 1995), red kangaroos (*Macropus rufus*; Munn et al. 2006), muskox (*Ovibos moschatus*), reindeer (*Rangifer tarandus*; Eisfeld 1990), northern brown bandicoot (*Isodon macrourus*; Young and Hume 2005), and bats (Studier et al. 1994). Not all of those studies provided direct correlates to dietary quality, demography, or behavior. For example, general feeding strategies (e.g., carnivore, frugivore) of Neotropical monogastric bats were simply inferred from levels of N and other minerals in feces, not by direct statistical analyses (Studier et al. 1994).

### FN Misapplications and Secondary Plant Compounds

Study designs of published research using FN varied, but most focused on single species in similar habitats in single ( $n = 26$ ) or multiple study areas ( $n = 7$ ; Table 5). The former

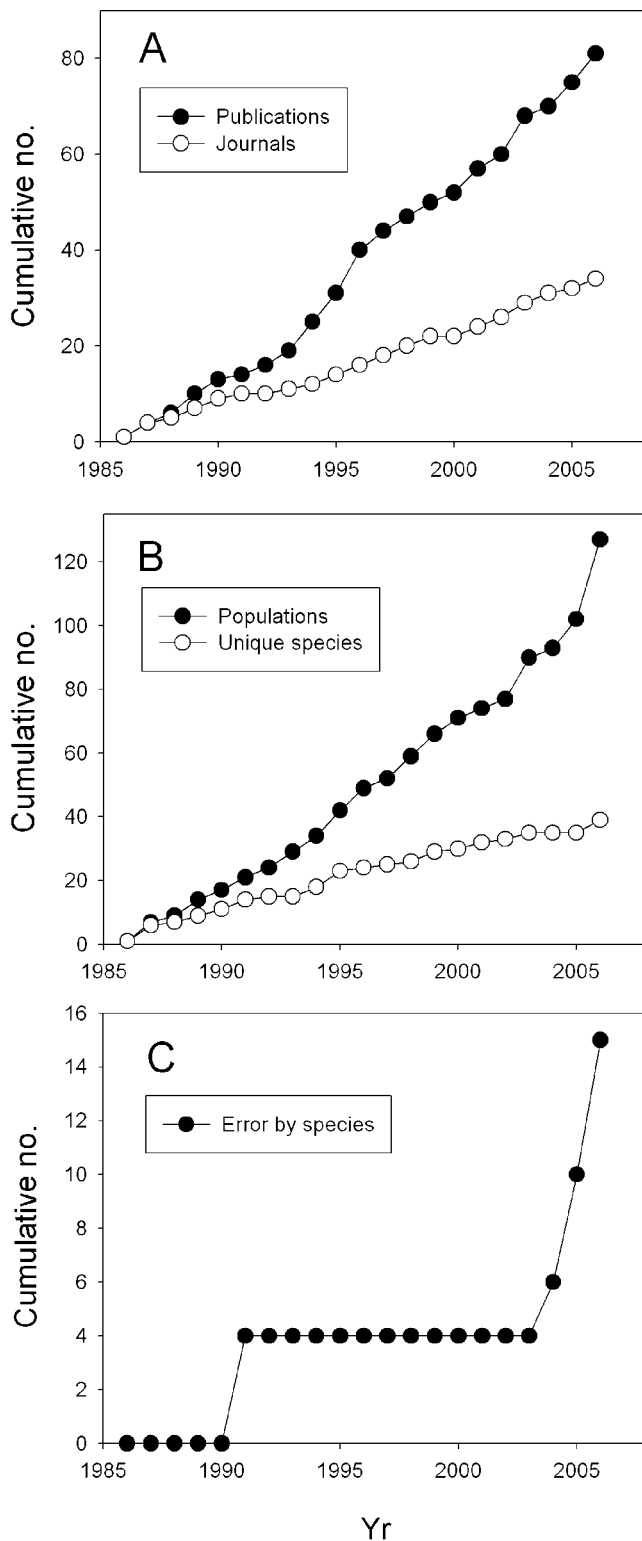
represented conditions considered earlier to be most favorable for FN applications (Leslie and Starkey 1987). Studies comparing multiple species ( $n = 11$ ), although less common (Table 5), resulted in the greatest number of misapplications of FN methodology (Table 2).

Criteria to judge the appropriateness of FN applications are straightforward if multiple species with differing digestive efficiencies are involved. We identified a recent increase in the number of interspecific misapplications since 1987 (Fig. 1C), whereas the application of FN remained relatively steady for the past  $\geq 20$  years (Fig. 1A). We identified 5 studies involving various comparisons among 13 unique species (Table 2), with 19 cumulative misapplications (Fig. 1C; Dunbar and Bose 1991; Kamler et al. 2004; Kamler and Homolka 2005; Codron et al. 2006a, b), rendering conclusions, and likely management recommendations, suspect.

Of the 87 publications citing the 3 *JWM* publications, 5 (5.7%) had specific objectives designed to evaluate effects of plant secondary compounds on various fecal parameters, including FN (Robbins et al. 1987, Leite and Stuth 1990, Nunez-Hernandez et al. 1992, Hodgman et al. 1996, Osborn and Ginnett 2001). Additionally, Irwin et al. (1993) used tannin-free diets in trials with captive bighorn sheep but did not specifically evaluate effects of tannins on FN.

## DISCUSSION

We realize that use of FN does not necessarily reflect value, but the number of published applications during the past 22 years indicates that peer reviewers of literature from a notable variety of scientific disciplines view FN as an acceptable proxy for nutritional status, which can be used to contrast study units when carefully defined by the study



**Figure 1.** Cumulative changes in the application of fecal nitrogen as an index of nutritional ecology as outlined in Leslie and Starkey (1985, 1987) and Hobbs (1987) highlighting (A) numbers of publications (i.e., studies) and journals, (B) numbers of populations and unique species studied, and (C) number of misapplications (we tallied a species more than once if it was involved in separate studies), January 1986–July 2007.

design. Nevertheless, any index can have shortcomings, and we caution that there are still circumstances when application of FN is problematic and must be done so to minimize shortcomings. In the following sections, we discuss the weight of evidence from published studies to judge appropriateness of application and whether consumption of plant secondary compounds, in and of itself, diminishes the value of FN. We focus on ruminants because most FN applications have occurred within that taxon.

### Misapplications of FN

Excretion of metabolic FN is considerably higher in ruminants and cecal digesters than it is in monogastric species where the absolute volume of microbial fermentation is considerably lower (Robbins 1983, Van Soest 1994). Therefore, comparisons of FN from species with disparate digestive capabilities do not provide useful insights on dietary N because differences basically result from physical and physiological differences among species rather than from dietary quality (e.g., Van Soest 1994). Studies that make such comparisons offer the clearest examples of misapplication of FN.

An early misapplication of the FN index occurred in Dunbar and Bose (1991), who compared 2 baboon species (*Theropithecus gelada* [graminivore] and *Papio anubis* [frugivore]), Burchell's zebra (*Equus burchelli*), and domestic cattle. After demonstrating a statistical difference in FN between baboons and other species and assuming that "both nutrient intakes and the digestibilities of the various nutrients [were] identical," Dunbar and Bose (1991:4–5) concluded that the 4 species differed in their abilities to extract protein from their food. Clearly, this is tautological because Dunbar and Bose (1991) could have made that conclusion based simply on digestive, physiological, and dietary differences among the species alone. To their credit, Dunbar and Bose (1991) did not directly conclude that one species consumed a diet higher in N than another based on FN alone. Nevertheless, fecal samples were collected in disparate habitats with different rainfall patterns, in different countries, and at different times but during the same season, a compromising design relative to inferring much about interspecific differences. The cautionary papers by Hobbs (1987) and Leslie and Starkey (1987) were not cited in this work.

Confirming that near-infrared spectroscopy is a valid method to measure N in feces, Kamler et al. (2004) concluded that differences in FN of European roe (*Capreolus capreolus*) and red deer in the Czech Republic alone supported the hypothesis that European roe selected a diet higher in N than did red deer. Although the conclusion of Kamler et al. (2004) has theoretical appeal, in a subsequent publication, Kamler and Homolka (2005:89, 94) conceded that direct comparisons of "different feeding specialists" was "unwise" but made numerous direct statistical comparisons anyway. In fairness, Leslie and Starkey (1985:143–144) took the same contradictory approach by statistically comparing Columbian black-tailed deer and Roosevelt elk and then cautioned that differences may not reflect N intake because "small ruminants have . . . higher fermentation rates, greater

**Table 3.** Nutritional, ecological, behavioral, and demographic variables correlated with fecal nitrogen in 26 methodological and field-based studies in which Leslie and Starkey (1985 [included below], 1987) and Hobbs (1987) were referenced in any combination, January 1986–July 2007.

Application type	Variable <sup>a</sup>	Range of <i>r</i>		References	
		Min.	Max.		
Methodological <sup>b</sup>	Dietary N	+0.50	+0.94	Loeb and Schwab 1989, Nunez-Hernandez et al. 1992, Irwin et al. 1993, Hodgman et al. 1996, Jhala 1997, Wrench et al. 1997, Mésochina et al. 1998, Osborn and Ginnett 2001	
	Dietary DN	+0.77	+0.87	Hodgman et al. 1996	
	Dietary DE	+0.93	+0.95	Hodgman et al. 1996	
	Dietary DEI	+0.90	+0.92	Hodgman et al. 1996	
	Dietary DMD	+0.79	+0.87	Loeb and Schwab 1989, Irwin et al. 1993, Jhala 1997, Mésochina et al. 1998, Osborn and Ginnett 2001	
	Dietary DMI	+0.86	+0.88	Hodgman et al. 1996	
	Dietary DOM	+0.49		Schmidt et al. 1999	
	Dietary fiber	-0.77		Mésochina et al. 1998	
	Daily weight gain		+0.84	Grant et al. 1996 <sup>b</sup>	
	Milk intake		+0.89 <sup>c</sup>	Cook et al. 1994	
	Solid food intake	-0.91 <sup>c</sup>	+0.89 <sup>d</sup>	Cook et al. 1994	
	Field-based	Dietary N	+0.58	+0.97	Leslie and Starkey 1985, Loeb and Schwab 1989, Irwin et al. 1993, Kamler and Homolka 2005, Ueno et al. 2007
		Dietary P	+0.84	+0.95	Leslie and Starkey 1985
		Dietary DMD	+0.76	+0.91	Leslie and Starkey 1985
Dietary DE		+0.62	+0.94	Kamler and Homolka 2005	
Dietary grass		-0.88	+0.53	Beier 1987, Codron et al. 2007	
Dietary forb		-0.62	+0.51	Branch et al. 1994, Massey et al. 1994	
Dietary browse		-0.76	-0.45	Beier 1987, Massey et al. 1994	
Dietary acorns		+0.60	+0.68	Massey et al. 1994	
Dietary oak leaves		-0.57		Massey et al. 1994	
Dietary chamise		-0.75		Massey et al. 1994	
Dietary <i>Artemisia</i> (winter)		-0.41	-0.68	Kucera 1997	
Dietary <i>Purshia</i> (winter)		+0.54	+0.80	Kucera 1997	
Dietary breadth (grass–forb)			+0.74	Branch et al. 1994	
Dietary grass–forb			+0.54	Beier 1987	
Mixed diet <sup>e</sup>		-0.50		McKinney et al. 2006	
Fecal DAPA		+0.58	+0.87	Leslie et al. 1989, Kucera 1997 (winter only)	
Density		-0.71	-0.50	Asada and Ochiai 1999, Blanchard et al. 2003, van der Waal et al. 2003, Miyashita et al. 2007	
Neonate mass (Jun)			+0.45	Côté and Festa-Bianchet 2001	
Pellet mass		-0.54		Page and Underwood 2006	
Dry season body mass		-0.49		Codron et al. 2007	
Yearling F mass gain			+0.51	Blanchard et al. 2003	
Non-lactating ad F mass gain			+0.50	Blanchard et al. 2003	
Spring temp		-0.78		Blanchard et al. 2003	
Spring precipitation		+0.48			
Summer precipitation		+0.61	Blanchard et al. 2003		
Elevation		+0.59	Sakuragi et al. 2003		
Hypsodonty index	-0.58	-0.44	Codron et al. 2007		

<sup>a</sup> DE = digestible energy, DEI = digestible energy intake, DMD = dry matter digestibility, DMI = dry matter intake, DOM = digestible organic matter, N = nitrogen, DN = digestible nitrogen, NDS = neutral detergent soluble material, DAPA = 2,6-diaminopimelic acid of bacterial origin.

<sup>b</sup> Studies that used captive-wild or domestic species.

<sup>c</sup> For juv elk (*Cervus elaphus*) 8–13 weeks of age.

<sup>d</sup> For juv elk 20–25 weeks of age.

<sup>e</sup> % of combined sedges, lichens, moss, berries, seeds, and nuts in the diet.

bacterial nitrogen produced, and larger surface-to-volume ratio in the alimentary tract (Arman et al. 1975).”

Similar to Dunbar and Bose (1991), Codron et al. (2006a) and Codron et al. (2006b) basically concluded, in part, that different levels of FN across 4–6 species with various digestive strategies and capabilities, and overall mass, could result from differential intake of dietary protein. Furthermore, to various degrees, both papers compromised their conclusions by using study designs that incorporated dissimilar habitats resulting in distinctively different diets, particularly for basically monogastric baboons (Codron et al.

2006b). Both papers also presented levels of fecal isotopes, which have been applied increasingly to the study of ruminant nutrition (e.g., Post et al. 2001; Stewart et al. 2003; Treydte et al. 2006; Walter et al. 2006; Codron et al. 2005, 2007). Their relationships to FN and appropriateness of interspecific comparisons of isotopes in feces show promise and need additional research.

### Plant Secondary Compounds

Leslie and Starkey (1987) argued that additional research was needed to clarify effects of plant secondary compounds

**Table 4.** Nutritional, ecological, behavioral, and demographic variables not correlated ( $P > 0.05$ ) with fecal nitrogen in 10 methodological and field-based studies in which Leslie and Starkey (1985, 1987) and Hobbs (1987) were referenced in any combination, January 1986–July 2007.

Application type	Variable <sup>a</sup>	References <sup>b</sup>
Methodological	Milk intake <sup>c</sup>	Cook et al. 1994
	Solid food intake <sup>c</sup>	Cook et al. 1994
Field-based	Density (May, Oct–Dec)	van der Waal et al. 2003
	Non-yearling and ad F mass gain	Blanchard et al. 2003
	Neonatal mass (Jul)	Côté and Festa-Bianchet 2001
	Fecal DAPA (spring)	Kucera 1997
	Fecal P	McKinney et al. 2006
	Fecal NDF	McKinney et al. 2006
	Various dietary components (%)	
	Individual forage classes	McKinney et al. 2006
	Mix of browse–forb–grass	McKinney et al. 2006
	Mix of grass–forb	Massey et al. 1994
	Grass	Massey et al. 1994
	Forbs	Massey et al. 1994, McKinney et al. 2006
	Browse	Beier 1987, Massey et al. 1994, Oehler et al. 2003, McKinney et al. 2006
	<i>Artemisia</i> and <i>Purshia</i> (spring)	Kucera 1997
	<i>Juniperus</i> berries and browse	Beier 1987
	<i>Quercus</i>	Beier 1987
	Acorns	Massey et al. 1994
	Mushrooms	Beier 1987
	Misc. fruit and seeds	Beier 1987
	Plant cover by forage class	Branch et al. 1994

<sup>a</sup> DAPA = 2,6-diaminopimelic acid of bacterial origin, P = phosphorus, NDF = neutral detergent fiber.

<sup>b</sup> Note that all references in this table provided significant correlates to FN summarized in Table 3.

<sup>c</sup> For juv elk 14–19 weeks of age.

on the utility of FN as a viable index of dietary N. Since 1987, considerable research and syntheses were accomplished on plant secondary compounds, particularly condensed tannins (e.g., Ayres et al. 1997, Makkar 2003), but relatively little of it focused on wild species and most of it was conducted in vitro (Dearing et al. 2005, Shimada 2006). Nevertheless, some of that research provides useful insight on effects of plant secondary compounds on FN.

First, we acknowledge that FN is affected by dietary characteristics other than plant secondary compounds. Brown et al. (1995) cautioned that FN should be used with insight on dietary composition because levels of not only protein but also energy influenced FN. For example, low-energy artificial diets, formulated from alfalfa, sorghum, cottonseed, corn, oats, and molasses, fed to white-tailed deer resulted in lower FN than did high-energy diets (Brown et al. 1995). Using diets similarly formulated but containing

leaves of southern live oak (*Quercus virginiana*), Osborn and Ginnett (2001) documented about 30% higher levels of FN in white-tailed deer consuming diets of high tannin–high protein compared with diets of high tannin–low protein. These constraints further support Hobbs' (1987) valid conclusion that site-specific FN–dietary N relationships should be established to permit prediction. Although these relationships merit further investigation with natural diets, we confine our discussion to research on relationships of FN and plant secondary compounds.

As highlighted by Hobbs (1987) and Leslie and Starkey (1987), ingested plant secondary compounds can elevate FN in ruminants irrespective of dietary N because under some circumstances (e.g., in the absence of tannin-binding salivary proteins; Juntheikki 1996, Shimada 2006), some of these compounds can bind insolubly with plant proteins, intestinal enzymes, and microbial residues, reducing overall protein digestion and increasing passage of N in the feces (Robbins et al. 1987). Nevertheless, studies on various plant secondary compounds and foraging–digestive strategies of herbivores have highlighted adaptations that minimize the toxic and protein-precipitating nature of such compounds (e.g., generalized diet, Dearing et al. 2000; large salivary glands, Robbins et al. 1995). For herbivores that consume such compounds, possessing adaptive mechanisms, singularly or in combination, to cope with plant secondary compounds would be expected. Discussing herbivores as if they all demonstrate the same physiological responses to the myriad of plant secondary compounds (e.g., Ayres et al. 1997, Shipley and Felicetti 2002) is not useful; some evidence indicates that “a gradient of adaptation” exists

**Table 5.** Characteristics of field studies of free-ranging wild and domestic species citing Leslie and Starkey (1985, 1987) and Hobbs (1987) in which fecal nitrogen was used as an index of nutrition relative to single or multiple species, type of study area, and season, 1986–2006.

Study focus	Type of study	Time of yr	Habitat similarity	
			Similar	Dissimilar
Single species	Single study area	1 season	3	0
		>1 season	26	1
	Multiple study areas	1 season	5	1
		>1 season	7	4
Multiple species	Single study area	1 season	1	0
		>1 season	3	0
	Multiple study areas	1 season	1	0
		>1 season	3	4

among herbivores to deal with ingested plant secondary compounds (Robbins et al. 1991:484–485).

Earlier studies cited repeatedly on the pernicious effects of plant secondary compounds on FN are worth careful review to ascertain if conclusions are still germane based on recent investigations. Mould and Robbins (1981) clearly demonstrated that when plants containing high levels of plant secondary compounds represented 33% and 100% of the diet of a captive elk, protein digestibility was decreased and FN was increased. Importantly, levels of FN resulting from an experimental diet with 33% fireweed (*Epilobium angustifolium*) and only 2 other grasses (unlikely a realistic diet of a free-ranging herbivores under normal conditions) were 84% lower than FN resulting from a 100% fireweed diet; levels of FN resulting from similar concoctions with maple (*Acer* spp.) leaves were 75% lower (we extrapolated values from Mould and Robbins 1981, fig. 2). At the 33% dietary level, FN was increased 23% for fireweed and 15% for maple leaves above the regression line of the overall FN–dietary N relationship. Such variability would not be useful for a precise prediction of N intake in, for example, balanced nutrient trials, but it would not be unexpected under field conditions and would not necessarily hamper the usefulness of FN to compare particular study units.

Osborn and Ginnett (2001) evaluated effects of high levels of condensed tannins in leaves of southern live oak on white-tailed deer fed low N (1.6% dry wt) and high N (3.2%) diets. Captive deer were fed diets formulated with 0%, 20%, or 40% oak leaves and 6 other ingredients including alfalfa hay, corn, and molasses. Tannin-based diets only increased FN when dietary N was high, and furthermore, FN increased only 13% and 22% for diets with 20% and 40% oak leaves, respectively (we extrapolated values from Osborn and Ginnett 2001, fig. 2). Similar effects, sometimes more pronounced, have been noted for other, typically, browse species known to be high in plant secondary compounds, yet consumed by free-ranging ruminants. For example, although percent FN values were not presented, guajillo (*Acacia berlandieri*) at 25%, 50%, and 75% of the diet, fed singly or mixed with hay to captive white-tailed deer and domestic goats, increased N loss in the feces and reduced digestibility with no differences in dry matter intake (Barnes et al. 1991, Nantoumé et al. 2001, Campbell and Hewitt 2005). As such, researchers need to be aware of such effects when establishing their study designs. Yet, how often do ruminants consume diets composed of 40%, or even 75–100%, of one forage rich in plant secondary compounds with only a few other, mainly agricultural, plant species? We conclude rarely, aside from some circumstances during seasonal extremes such as heavily browsed winter deeryards (Hodgman and Bowyer 1986) or during extended drought.

Most often, individual plant species comprise far less than 33–40% of a typically diverse diet of a ruminant, which minimizes, based on the work by Hodgman et al. (1996), elevation of FN by plant secondary compounds. Hodgman et al. (1996, table 1) formulated mixed seasonal rations with

up to 15 largely native plants and plant parts (i.e., browse leaves and stems) for their experiments with 2 mule deer subspecies, which more accurately depicted diets of free-ranging ruminants and consumption of plant secondary compounds than narrowly formulated experimental diets. Notably, winter diets of 60–100% browse were the only formulations that contained measurable amounts of tannins but averaged only 0.156 bovine serum albumin (BSA)/mg (tannin index as precipitate of BSA; Robbins et al. 1987) compared to 0.50–0.84 BSA/mg for fireweed and 0.41 BSA/mg for maple (McArthur et al. 1993). Critical to our argument, Hodgman et al. (1996) were unable to detect influences of tannins on fecal indices when mule deer were fed these realistically formulated diets.

Effects of plant secondary compounds on FN rarely have been evaluated with experimental diets that realistically mimic diets of free-ranging individuals, and differences are to be expected in the FN–dietary N relationship when experimental diets are narrowly formulated. While feeding low- and high-phenolic diets to cattle and goats, Nunez-Hernandez et al. (1992) noted that controlled feeding trials only provided insights into sharp contrasts in diets but did not mimic the typically diverse diets of free-ranging ungulates that change gradually with phenology and availability. Therefore, Nunez-Hernandez et al. (1992:147) concluded that their limited success in predicting dietary quality with fecal parameters did “not invalidate” studies that “have shown fecal nitrogen concentrations [as] useful indicator[s] of grazing ruminant nutritional status.” When diverse mixtures of wild-grown forages are fed to captive ruminants, FN appears to be a reliable index of dietary quality, likely because the influence of tannins in diverse diets is diminished or eliminated (Hodgman et al. 1996).

Robbins et al. (1987:103) leveled the harshest criticism of FN by concluding that it “should not be used in ecological studies” because it “is not a precise indicator of either dietary nitrogen or dry matter digestibility.” Robbins et al. (1987) based their conclusion on variability in an FN–dietary N relationship constructed from 9–10 studies on 3 North American ruminants (Robbins et al. 1987, fig. 9), presumably fed forage class-specific diets of unknown composition because paired observations in their figure depict levels of FN and dietary N, for example, of grasses, legumes, and high-phenolic leaves and flowers. Given data from such variable sources and no doubt variable methodologies, we would not expect much precision at all, but we did note that if outlying high-phenolic leaves and flowers were omitted, variability of the relationship would be reduced. No definition of what represents acceptable precision (e.g.,  $r^2$ -values) for the FN–dietary N relationship was provided by Robbins et al. (1987) or Hobbs (1987). Nunez-Hernandez et al. (1992) set their level of acceptable precision at  $r^2 = 0.80$ , but others, no doubt, will have different expectations.

Hobbs (1987) was particularly concerned about high intra-seasonal variability and opined that an FN–dietary N relationship developed for one site was not generally

predictive at other sites, which is indeed a limitation of FN applications because such relationships are site specific and should not be used predicatively elsewhere. Field applications of FN in the past 22 years, however, generally were not concerned with a prediction of intake of N or some other nutrient. Investigators assumed that FN adequately indexed the relative nutritional state of their study animals, even within one season, and then compared FN levels, for example, of populations and study sites (e.g., Jenks et al. 1996). We conclude that this is still an adequate application of FN (Leslie and Starkey 1987), and results can represent basic ecological differences among study units and through time (e.g., Blanchard et al. 2003, Ueno et al. 2007).

Theoretically, herbivores consuming large amounts of tanniniferous forage should possess adaptations to counter any negative effects. Jones et al. (2001), however, did not find *in vitro* evidence for the hypothesis that ruminal microflora of browsing ungulates were better equipped to handle tanniniferous forages than those of grazing ungulates and opined, in keeping with Robbins et al. (1991) and Shimada (2006), that binding of ingested tannins with proline-rich saliva may differentiate species that can consume diets high in tannins without ill effects. Of note, salivary proteins of mule deer reduced FN losses per unit of tannin ingested (Robbins et al. 1991). Tannins, and other plant secondary compounds, are remarkably diverse in their structure, occurrence, and potency and are very abundant in typical ecosystems (Ayres et al. 1997). Some tannins, in particular amounts, may even enhance microbial protein synthesis and subsequent absorption beyond the rumen, or protect “feed proteins from degradation in the rumen, leading to increase in the flux of essential amino acids to small intestine and increase in the absorption of essential amino acids to blood” (Makkar 2003:243).

To us, these observations indicate that plant secondary compounds in diets do not automatically increase FN of a ruminant, and mixed diets can ameliorate effects on such compounds. As Ayres et al. (1997) articulated, the real value of secondary compounds to plants that spend considerable energy producing them is to deter consumption, not damage the consumer. Although it is beyond the scope of this paper, preference feeding trials confirmed that ruminants often are able to discern and avoid forages with pernicious levels of particular plant secondary compounds (e.g., Cooper and Owen-Smith 1985, Cooper et al. 1988, McArthur et al. 1993, Nantoumé et al. 2001). Therefore, the assertion of Hobbs (1987:319) that FN will “be elevated whenever diets contain tannins” can now be considered an overgeneralization.

### Recent Appropriate Applications

We agree with Brown et al. (1995) that study designs that use >1 index of nutritional status provide more insight than those using one index. In 47 of the field-based applications of FN (Table 2), investigators used FN along with other indices to substantiate their contrasts of study units, which was prudent. Nevertheless, we contend that 4 recent studies successfully used FN alone with careful attention to study

design and application limitations (Blanchard et al. 2003, Sakuragi et al. 2003, van der Vaal et al. 2003, Miyashita et al. 2007). Relative to the cautions by Hobbs (1987), recommendations by Leslie and Starkey (1987), and research results since 1987, we believe that it is useful to highlight recent examples from the literature that used study designs and protocols that were logical approaches to any concern over secondary compounds and that provided constructive insights on ecology and management on the species of interest.

Oehler et al. (2003) provided a reasonable way to address possible affects of secondary compounds while still permitting comparison of 2 populations of bighorn sheep inhabiting dissimilar habitats with disparate precipitation patterns in the Mojave Desert of the southwestern United States. Oehler et al. (2003) used a variety of indices and demonstrated significant differences in the cover of forage types, particularly shrubs, perennial forbs, and grasses, between the 2 study areas, which was reflected in disparate nutrient availabilities to bighorn sheep. Differences in FN between the 2 areas were interpreted to reflect higher dietary quality and not the influence of plant secondary compounds because there was no relationship between levels of FN and proportions of shrubs (known to be high in secondary compounds) in the diets. Density of females, home-range size, forage quality, and climatic variability in their study paralleled their conclusion of disparate nutritional levels between study populations.

The study by van der Waal et al. (2003) evaluated nutritional ecology of 8 populations of greater kudu (*Tragelaphus strepsiceros*) confined by game fences to units of 750–4,588 ha in northwestern South Africa. Van der Waal et al. (2003) were interested in assessing density (2.3–6.3 kudu/100 ha), physical condition and mortality, and supplemental feeding (3 of 8 units) relative to kudu nutrition and used FN as their nutritional proxy. All units were shrub lands dominated by the deciduous shrub *Grewia* spp., but each had somewhat different subdominant shrubs. Levels of FN and density of kudu were correlated negatively during the dry season (Table 3), poor physical condition and high mortality were associated with low FN, and FN reflected positive aspects of some supplemental feeding. As expected, there were no relationships of FN and density in May and October–December when forage availability was high. Any possible role of plant secondary compounds was reasonably addressed by assuming consistent effects among study units (cf. Leslie and Starkey 1987).

Between 1987 and 2005, FN was used to elucidate aspects of sexual segregation hypotheses (Main et al. 1996, Bowyer 2004) among ungulates (Beier 1987, Bleich et al. 1997, Post et al. 2001, Mooring et al. 2005). Although Bleich et al. (1997) did not cite the 3 *JWM* papers, they used the same rationale as Oehler et al. (2003) when considering effects of tannins on FN, noting that there was no relationship between percentage of shrubs (high in tannins) in the diet and FN for either male or female bighorn sheep. Under normal precipitation patterns, male bighorn sheep exploited

habitats of higher quality than females, as indexed by FN, thereby maximizing body condition, horn growth, and likely fitness. Recent FN applications on bison (*Bison bison*) showed the opposite trend in that males generally consumed diets of lower quality but from habitat with more abundant forage (nutritionally advantageous relative to male mass) during segregation than did females and calves (Post et al. 2001, Mooring et al. 2005). Both studies used FN to claim support for the sexual dimorphism–body size hypothesis related to sexual segregation among ungulates (Main et al. 1996), albeit that hypothesis was questioned recently (Bowyer 2004).

### Future Application

Multispecies applications of FN are most problematic and should be avoided. Direct comparison of species with very different digestive capabilities to elucidate disparate nutritional ecologies can lead to erroneous interpretations. Interspecific comparisons with FN that we identified as resulting in faulty conclusions were infrequent for most of the past 22 years; 80% of them occurred in 2004–2006. Regardless, this is an undesirable trend that may lead to further misapplication of the FN index if such studies are cited as justification for new investigations.

After re-evaluation of early concerns over the use of FN relative to plant secondary compounds (Hobbs 1987, Robbins et al. 1987) and evaluation of subsequent research that addressed this issue experimentally, we suggest that such effects have been overextended from studies of captive ruminants consuming unrealistic, even monotypic, diets. We observed little evidence of overly elevated FN of ruminants consuming diverse diets, typical of most free-ranging conditions, but encourage more research with naturally formulated diets. As Brown et al. (1995) concluded, however, basic knowledge of dietary trends is useful to identify unique conditions under which FN could be elevated by a particular plant species containing high levels of plant secondary compounds (e.g., Mould and Robbins 1981, Osborn and Ginnett 2001, Campbell and Hewitt 2005). When FN levels differ for a single species among study units (Leslie and Starkey 1987), it is reasonable to conclude that they index real differences in nutrient intake that can be reflected in condition, demography, or behavior.

Most concern over FN is expressed by those who want a precise predictor of intake of nitrogen or some other nutritional dietary characteristic. We agree that the predictive ability of FN is diminished empirically by the complexity of ingestion, digestion, and excretion of nitrogen, and associated effects, for example, of digestibility (Wehausen 1995), energy and protein consumption (Brown et al. 1995, Osborn and Ginnett 2001), secondary plant compounds (Robbins et al. 1987), and seasonal interactions with habitat treatment (Ruthven et al. 1994). In contrast, other researchers seek an index to assess consequences in nutritional status, demography, or behavior among study units. They are cognizant of the complexity of FN, but they assume that FN accurately captures a nutritional snapshot useful for comparison. By analogy, wildlife practitioners

frequently use indices of body condition or demography that have complex roots in physiology, reproduction, and behavior, for example, but they do not overextend their use to prediction.

### MANAGEMENT IMPLICATIONS

We conclude that the protocols for FN application outlined in Leslie and Starkey (1987:324) are still applicable but amend them as follows. First, those protocols are applicable only to comparisons or contrasts among study units and not to applications where predictive capability is desired; prediction is still possible when established empirically, in advance, for a particular study area. Second, interspecific comparisons of species with disparate mass and digestive strategy should not be conducted with FN. Third, study design, subsequent conclusions, and management recommendations are strengthened by the use of multiple indices to evaluate any consequences of nutrition on life-history characteristics of herbivores.

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