

Research Article

Relationships Among Nutrition and Reproduction and Relevance for Wild Animals

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This review discusses aspects of feeding ecology, nutrition, and dietary husbandry that are particularly relevant to reproductive success in wild animals. Emphasis has been placed on recently published literature. Special attention has been given to requirements for energy and protein and the unique roles of essential amino acids, essential fatty acids, calcium, phosphorus, zinc, copper, selenium, and vitamins A, C, D, and E. Information has been drawn from research with mammals, birds, reptiles, amphibians, and fish, including the domestic and laboratory species that play such a large role in elucidating mechanisms connecting nutrition and reproduction. Zoo Biol 23:475–487, 2004. © 2004 Wiley-Liss, Inc.

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INTRODUCTION

Proper nutrition and dietary husbandry are fundamental to reproductive success. Because reproductive physiology and sexual behavior are so sensitive to the supply of metabolic fuels, when food intake is limited or an inordinate proportion of dietary energy is invested in physical activity or maintenance of homeostasis in an unfavorable environment, reproduction may be suspended in favor of metabolic processes that ensure individual survival (Wade et al., 1996). The variety of strategies employed by wild species to ensure survival in natural ecosystems poses comparable challenges for those seeking reproductive success in management of free-ranging or

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captive populations. Robbins (1993) discussed these for mammals and birds, and this reference provides a number of useful literature citations from which several of the following observations have been extracted.

Reproducing mammals must be adequately nourished to support vitality of ova and sperm, growth of reproductive organs, normal in utero development of the embryo and fetus, successful parturition, and production of immune globulins and nutrients in colostrum and milk. Reproducing birds require adequate nourishment for vitality of ova and sperm, development of embryos within eggs, and energy demands of incubation. Calcium is needed for the eggshell, as well as for soft tissue function and the development of embryonic skeleton. Even hummingbirds have been reported to ingest mineral-rich soil, eliciting speculation that this behavior may be a response to increased calcium needs for reproduction (Adam and Des-Lauriers, 1998). Precocial birds require little parental effort after hatching. Altricial birds require continuing parental care, and parental diets of some species must support production of crop "milk" to nourish the young. Reproducing reptiles are viviparous or oviparous. Viviparous reptiles have reproductive requirements similar to mammals but without the nutrient demands of milk production. Oviparous reptiles have reproductive requirements similar to birds. Although hatchling oviparous reptiles are not fed by their parents, some have an extended period of parental protection from predators. Some reproducing amphibians are oviparous (as are fish), but they do not produce a mineralized eggshell. Other amphibians may exhibit a primitive viviparity (Greven, 1998) or be ovoviviparous (i.e., retaining developing embryos in the oviducts and giving birth at various stages of development without maternal nutrition beyond that in yolk) (Wake and Dickie, 1998). Parental responsibilities of amphibians and fish vary widely among species.

Environmental Effects on Nutrient Supply

Seasonality of reproduction in many animal species appears to represent an accommodation to environmental variables that influence reproductive success. Among those variables is the available food supply, which tends to be limited in the wild during periods of drought or cold. This is illustrated by relations between reproductive timing and seasonal shifts in prey consumption by mulgara (*Dasycercus cristicauda*) in the Simpson Desert in Queensland, Australia (Chen et al., 1998) and in amounts and quality of browse consumed by black rhinoceroses (*Diceros bicornis minor*) in Zimbabwe (Garnier et al., 2002). Gender differences in the inhibitory effects of declines in ambient temperature and reduced food supplies upon reproduction have been observed in the South African rodent, *Rhabdomys pumilio* (Jackson and Bernard, 2001). In males, both reduced ambient temperature and reduced quantities of food inhibited spermatogenesis and mass of reproductive organs. In females, only food restriction inhibited reproduction, reducing the masses of the ovaries and uterus, the development of the uterine wall, and the numbers of developing follicles and corpora lutea. Sexual size dimorphism as affected by population density and resource availability has been studied in bighorn sheep (*Ovis canadensis*) (Leblanc et al., 2001). Population density was found to negatively affect seasonal mass changes in young males and females, but this effect gradually disappeared in females, apparently as a consequence of compensatory growth. Males, however, showed

a lifelong effect, and these researchers proposed that female bighorn sheep have greater flexibility than males in resource allocation to growth or reproduction.

Studies of the relation between maternal nutrition and sex ratio of offspring of higher life-forms tend to be equivocal. However, prepubertal fallow deer (*Dama dama*) that were fed low ($n = 29$; 10 MJ/kg DM) or high ($n = 29$; 12.5 MJ/kg DM) energy diets during their first winter (4–10 months of age) gave birth to 46% or 75% males, respectively ($P < 0.05$; Enright et al., 2001).

The neuroendocrine mechanisms by which food restriction limits reproduction have been studied in male prairie voles (*Microtus ochrogaster*) (Kriegsfeld et al., 2001). After 2 weeks of restriction to 70% of daily mean ad libitum food consumption, there was an increase in gonadotropin releasing hormone-immunoreactive (GnRH-ir) neurone soma size. After 3 weeks, there was a pronounced increase in GnRH-ir neurone numbers and an increase in fiber intensity in the main fiber pathway to the median eminence. These modifications led to a temporary cessation of reproduction without pronounced changes in reproductive organ morphology and may provide a mechanism for rapid reinitiation of breeding when the environment once again provides sufficient food. A positive relation between seasonal changes in testicular size and serum concentrations of LH, prolactin, and testosterone has been observed in free-ranging male polar bears (*Ursus maritimus*) in northern Canada (Howell-Skalla et al., 2002). These values tended to be highest in April during the breeding season and lowest in October during the nonbreeding season. Whether these differences were related to available food resources was not established. It should be noted that some wild ruminants exhibit seasonal changes in antler development that are related to serum concentrations of testosterone and prolactin. In the spring, when testosterone and prolactin concentrations are low, old antlers are shed and new ones begin to grow. Under these circumstances, the antler-producing cells in the pedicel are sensitized to the growth-stimulating effects of IGF-1. These hormonal changes are presumed to be a consequence of photoperiodic signals by way of melatonin secretion by the pineal gland. However, when population density is high enough to limit food resource availability, antler development can be inhibited, particularly in young males (Santiago et al., 2001). An interesting adaptation, ensuring survival and reproduction despite seasonal changes in amounts and quality of the food supply, has been observed in pikas (*Ochotona curzoniae*) on the Qinghai–Tibetan Plateau (Wang and Wang, 2001). Masses and linear dimensions of the stomach, small intestine, large intestine, and cecum were measured at time of plant green-up (May), maximum plant growth (July), and plant senescence (October). Measures of the empty stomach changed little with season, but the small intestine was larger during periods of maximum plant growth and senescence, and the large intestine was longer and the dry weight of the cecum greater during the period of senescence. These researchers suggested that adjustments in the capacity of gastrointestinal segments may play an important role in the accommodation of the pika to changes in amounts and quality of food resources. As a consequence of increased absorptive area and microbial activity, the pika might be able to extract a higher proportion of energy and nutrients from food resources than if these anatomical adjustments had not occurred.

Expressing Energy and Nutrient Requirements

Quantitative requirements of animals for energy and nutrients are commonly expressed in units/day or units/kg of dietary dry matter (DM). Expressing requirements for various biological functions in units/day is considered to be the most accurate because metabolic needs for energy and nutrients are time-dependent, and this expression is not subject to variations in food intake (National Research Council, 1981; Robbins, 1993). However, except for maintenance of adult animals in a thermoneutral environment, daily requirements can change rapidly with time as affected by environmental extremes of cold or heat or the extra demands of growth or reproduction. In contrast, changes in requirements for special biological functions expressed in units/kg of dietary DM occur more gradually, in large degree because animals with ad libitum access to food will adjust food intake in proportion to changing daily nutrient needs. If controlled amounts of food are offered each day, animal caretakers must assume responsibility for adjusting these amounts to ensure that changing needs for special circumstances, such as the onset of cold weather or the demands of fetal growth or lactation, are met.

Requirements for Reproduction

Requirements for reproduction demand food intakes above those for maintenance, although tissues of reproducing adults may be mobilized in the short-term (and replaced later) to meet immediate nutrient and energy needs for fetal development or for egg or milk production. By measuring growth of maternal tissues and the products of conception, one can compute some of these extra requirements. However, specialized behaviors such as courtship, territorial defense, and burrow- or nest-building, plus the search for food to feed the young also add appreciably to reproductive requirements, particularly in the wild (Robbins, 1993).

Most of the costs of reproduction in mammals are related to the amounts of energy and tissue accumulating in the gravid uterus and enlarging mammary glands. Of the energy retained by the gravid uterus, about 80% is in fetal tissue (Robbins and Moen, 1975; Kurta et al., 1989). The relation between birth weight (Y) and maternal weight (X) is exponential (average of 0.76; $Y = nX^{0.76}$), and larger species produce young that represent increasingly smaller proportions of adult weight than do young of smaller species (Robbins, 1993). However, there may be important differences in fetal composition between species that comparisons of fetal weight do not reveal. In any case, energy requirements and food intakes are about 17–32% higher in pregnant than in nonpregnant females. Energy requirements for lactation are higher still—2–3 times higher than requirements for gestation or about 4–7 times basal metabolic rate (BMR).

The requirements above maintenance for egg production in birds are proportional to the energy and protein content of the egg, the number of days required for its synthesis and deposition, and the number of eggs produced per clutch. Hawks and owls lay an egg about every third day, with an average clutch size of five. Energy requirements for egg production are about 29% above BMR, and protein requirements are about 72% above maintenance. Waterfowl, gulls, and terns lay a rather high-energy egg each day until a clutch size of 5–12 is reached. Energy requirements for egg production by these birds are 100% to >200% above BMR, and protein requirements are about 220% above maintenance. These high energy

and protein demands are met by accumulating body fat before reproduction, mobilizing body fat and protein during egg laying, increasing food intake and selecting nutrient-rich items, and by reducing other nonessential costs. Energy costs for incubation vary with size of the incubating adult, clutch size, insulating quality of the nest, and the ambient temperature. A main cost is the reduced time for feeding; parents with sole responsibility for incubation or with prolonged incubation times lose very significant amounts of weight (Robbins, 1993).

Energy expenditures for reproduction as compared with maintenance have been estimated in Adelie penguins (*Pygoscelis adeliae*) at Palmer Station, Antarctica (Chappell et al., 1993). Adelie breeding behavior includes courtship (when both sexes fast), incubation, the "guard" stage (when chicks are from 1 to 18–28 days of age), and the "crèche" stage (from end of guarding until chicks are 38–45 days of age). Both sexes lost a considerable amount of their prereproduction mass during the initial stages of the reproductive season, with males fasting longer and losing more mass. The mass losses in both sexes were composed of 66% depot fat and 34% lean tissue. Metabolic energy expenditures for foraging to replace the mass lost during fasting were 63 MJ in males and 39 MJ in females. The metabolic energy expenditures associated with feeding the chicks were 31 MJ for males and 36 MJ for females. Thus, the cumulative reproductive energy expenditure was about 94 MJ in males and 75 MJ in females, or 5.3–6.2% of the annual energy budget.

Effects of Nutrient Restriction

Reproduction in Syrian hamsters (*Mesocricetus auratus*) is sensitive to the availability of metabolic fuels. Estrous cycles can be interrupted by brief periods of food deprivation, a phenomenon mimicked by increased energy demands for thermoregulation or by pharmacological inhibition of glycolysis and fatty acid oxidation (Wade et al., 1991). Further study suggests that central nervous system glucose deprivation but not peripheral lipid deprivation is a critical feature of this inhibition in hamsters (Schneider et al., 1997).

Nutrition during nonreproductive or nonlactating periods and its potential for influencing reproduction have been extensively studied in domestic ruminants, particularly in dairy cattle (National Research Council, 2001). Whereas inappropriate dietary husbandry (including excessive energy intakes) during the transition from nonlactation to lactation may lead to metabolic disorders in the cow, insufficient energy during dry (nonlactating) periods can result in unthrifty, light-weight calves at birth. A deficiency in protein slows growth rate of the fetus, results in small calves at birth, and, if severe enough, lowers immune globulin concentrations in colostrum. Iodine deficiency results in newborn calves with goiter, and selenium deficiency results in calves with degenerative changes in cardiac and skeletal muscle. A deficiency of vitamin E produces signs similar to those of selenium deficiency, and affected calves may have difficulty standing or be unable to suckle. Vitamin A deficiency results in abbreviated gestation periods, abortions, or birth of uncoordinated, blind, or weak calves that are prone to chronic diarrhea.

Effects on the lifetime reproductive performance of female sheep at two levels of food intake during the preweaning period or during adult life were investigated with 499 Brecon Cheviot sheep. Normally, this breed shows only a small reproductive response to contemporary nutritional manipulations. Female sheep that were nutritionally restricted before weaning had a significantly lower lifetime

production of multiple births than those on a high plane of nutrition. No such difference was apparent when the nutritional restriction was imposed during adult life (Rhind et al., 1998).

Research with sheep has demonstrated that ewes underfed during pregnancy produce fetuses that exhibit both morphologic and metabolic perturbations. Fetal organ weights and skeletal dimensions are affected, although not always as expected. Fetuses from underfed ewes have lower plasma glucose, insulin, and IGF-I levels, and higher levels of plasma IGF-binding protein-2 (Osgerby et al., 2002). Poor fetal growth due to maternal food restriction during pregnancy in rats was found to be associated with decreased pancreatic beta-cell mass at birth and glucose intolerance in adulthood (Blondeau et al., 2001). Increased maternal and fetal corticosterone levels occurred as a consequence of maternal undernutrition, and it was concluded that glucocorticoid overexposure mediated the effect of undernutrition on beta-cell mass.

The influence of maternal undernutrition upon specific features of fetal gonadal development is an active current area of investigation. Research has shown that the reproductive performance of animals as adults can be determined in part by factors affecting various stages of their in utero development from before conception until after birth. It has been postulated that these effects are mediated through the hypothalamic-pituitary and gonadal axes, with the system affected dependent on the stage at which the influence is applied (Rhind et al., 2001). When pregnant domestic sheep were subjected to energy restriction during the first third of gestation, mean fetal mass was unaffected, but mean fetal ovarian mass was significantly reduced. There were fewer germ cells at the resting, diplotene stage of initial meiosis, characteristic of a delay in germ cell maturation and delayed onset of meiosis. Based on development of the granulosa cell layer at Day 110 of gestation, undernutrition before and during folliculogenesis appeared to delay fetal follicular development (Rae et al., 2001).

When female mice were food-restricted during gestation, the daughters of food-restricted mothers were equal to daughters of control mothers in the number that produced one or two litters, although the numbers of pups weaned in the second litters by daughters of food-restricted mothers (4.5 ± 0.65 [SEM]) were fewer than weaned by daughters of controls (5.9 ± 0.57 [SEM]) (Meikle and Westberg, 2001b). However, the reproductive success of sons of food-restricted mothers was more severely affected than that of daughters. This appeared to be caused in part by diminished testosterone synthesis in the male fetuses and a consequent impaired development of the seminal vesicles and coagulating glands (Lung and Cunha, 1981). In addition, sons of food-restricted mothers had lower body weights at weaning and as adults, were less frequently dominant in intrasexual agonistic encounters, and were less frequently preferred by estrous females (Meikle and Westberg, 2001a). Food restriction in 8–10-months of age male chickens causes reductions in body weight, semen ejaculate volume, sperm concentration, and progressive sperm motility (Omeje and Ude, 1998).

Seasonal changes in thyroid function have been measured over 2 years in desert tortoises (*Gopherus agassizii*) (Kohel et al., 2001). Plasma triiodothyronine was nondetectable, but plasma thyroxine (T4) concentrations exhibited distinct cycles in both sexes. T4 levels were lowest during hibernation and rose toward the time of emergence. Female T4 levels peaked in early spring and male T4 levels peaked in

early spring and again in late summer. Activity patterns of the desert tortoise include increased feeding, mating, and locomotor activity in early spring and increased mating and combat in late summer. When food was withheld from captive tortoises for 2 weeks, plasma T4 declined compared with that of fed tortoises and increased again within 36 hours of refeeding, indicating that thyroid activity was responsive to food intake. The second seasonal T4 peak seen in males was found only in reproductively active adults but not in subadults or juveniles.

Effects of Specific Nutrients

Protein and Essential Amino Acids

Neonatal rats born to protein-deficient mothers have fewer renal glomeruli than normal. When maternal diets containing 18, 9, or 6% protein were fed from the start of pregnancy, altered cell turnover was observed in the metanephros, the embryonic precursor of the adult kidney, in young of mothers fed the two lower protein diets. The increased apoptosis of mesenchymal cells at the start of metanephrogenesis may be responsible for the relative nephron deficits in these protein-deficient rats (Welham-Simon et al., 2002).

Evidence that dietary amino acid composition may limit egg production in free-living birds was demonstrated by provisioning breeding blue tits (*Parus caeruleus*) with two feed supplements that differed only in the concentration of five essential amino acids. Birds receiving the supplement containing protein with an amino acid mixture close to the amino acid composition of egg protein laid significantly larger clutches (18% larger) than control birds receiving an identical supplement except with protein that was less well balanced with respect to these five essential amino acids (Ramsay and Houston, 1998).

Essential Fatty Acids

Considerable attention is being given to the involvement of n-3 fatty acids in vital reproductive events. Increases in brain weight and active neurogenesis in late intrauterine life are characterized by rapid accumulation of docosahexaenoic acid (DHA, 22:6 n-3) in normal rat embryo brains. When an n-3 deficient diet was offered to female rats from gestation Day 1 to gestation Day 20, DHA concentrations in fetal brain were reduced by over 30%, counterbalanced by an increase in docosapentaenoic acid (DPA, 22:5 n-6). When a DHA-enriched triglyceride was fed to n-3 deficient dams on gestation Day 15, embryonic brain DHA concentrations were restored to normal in 48 hours. Although maternal reserves of DHA appeared sufficient to prevent major changes in brain phospholipid composition in this study, a longer period of n-3 depletion might be expected to adversely affect neurogenesis and brain function (Schiefermeier and Yavin, 2002).

Studies of domestic chicken semen have suggested that lipid and fatty acid components of spermatozoa may be important determinants of fertility. The phospholipids in duck spermatozoa were found to be high in the n-6 polyunsaturated acids, arachidonic (20:4 n-6), docosatetraenoic (22:4 n-6), and docosapentaenoic (22:5 n-6), with substantial amounts of the n-3 fatty acid docosahexaenoic (22:6 n-3) (Surai et al., 2000). Vitamin E concentrations were unexpectedly low in duck spermatozoa and seminal plasma compared with those in chickens, considering their potential for lipid peroxidation. However, there was evidence that increased seminal

plasma concentrations of superoxide dismutase (Cu-Zn) and glutathione peroxidase (Se) provided the duck spermatozoa with antioxidant protection.

Zinc

Effects of zinc (Zn) deficiency on testicular development have been studied in young Merino rams (initial mean weight 22 kg) (Martin et al., 1994). Diets containing 4, 10, 17, or 27 mg of Zn/kg were fed ad libitum (five rams on each diet). To control for the anorexia of Zn deficiency, an additional group of five rams was pair-fed a diet containing 27 mg of Zn/kg in amounts restricted to those consumed voluntarily by Zn-deficient rams (4 mg of Zn/kg). After 96 days, epididymal and testicular masses were not different between rams fed 10, 17, or 27 mg of Zn/kg, but were lower in pair-fed controls and lowest in the Zn-deficient rams. Testicular responsiveness to LH pulses, measured as pulses in plasma testosterone concentration, increased in all treatments except for rams fed 4 mg of Zn/kg diet. Development of the seminiferous tubules was retarded by food restriction but more severely by Zn deficiency. Effects of Zn deficiency appeared to be a consequence of both nonspecific and Zn-specific factors. Low feed intake, a nonspecific factor, resulted in low frequency of pulses of GnRH production by the hypothalamus, leading to low rates of gonadotrophin release by the pituitary. A Zn-specific response involved reductions in the capacity of the testes to synthesize or release testosterone or in testosterone binding by testicular receptors. This response led to impaired development and function of the seminiferous tubules.

Copper

Dietary copper (Cu) has been shown to be an essential trace element for reproduction in all species studied (Keen et al., 1998). Clinical signs of Cu deficiency in reproducing domestic cats include neonatal death, premature births, hypochromatrichia, and collagen abnormalities, manifested as twisted limbs and curled tails in newborn kittens. Cu requirements are influenced by bioavailability of the Cu source, but more than 5 mg of Cu/kg diet from CuSO₄ seems to be necessary for optimal reproduction in cats (Fascetti et al., 2000).

Selenium

In all animal species studied, selenium (Se) deficiency impairs reproductive performance of both males and females. In domestic chickens, egg production and hatchability are reduced (Cantor and Scott, 1974), and in Japanese quail (*Coturnix coturnix*), hatchability of fertile eggs and viability of newly hatched chicks are impaired (Jensen, 1968). In domestic pigs, litter size (Mahan et al., 1974), conception rate of gilts to first breeding (Edwards et al., 1977), and piglet mortality (Nielsen et al., 1979) were improved by adding supplemental Se to a low-Se diet. Low fertility, high embryonic mortality between 3 and 4 weeks after conception, and high neonatal mortality in domestic sheep in New Zealand and Australia have been corrected by Se supplementation when supplemental vitamin E alone was ineffective (Hartley, 1963; Wilkins and Kilgour, 1982). Retained placentas in dairy cows also can be an expression of Se deficiency (Julien et al., 1976).

Se deficiency has been shown to reduce fertility in both male mice and rats. Spermatogenesis may continue, but morphologic abnormalities appear in the midpiece of epididymal spermatozoa. The primary abnormality involves the shape

and arrangement of the mitochondria that form the midpiece sheath. A major function of Se during spermatogenesis involves synthesis of a cysteine-rich selenoprotein in the outer membranes of the sperm mitochondria. Maximal synthesis of this protein occurs approximately midway during spermatogenesis. In Se deficiency, mitochondrial capsules are abnormally fragile and misshapen, leading to a reduction in stability of the sperm tail. As a consequence, sperm count and fertility are sharply reduced even though some sperm motility may persist (Wallace et al., 1987).

Effects upon spermatogenesis of Se and vitamin E additions to the diet have been studied in domestic swine fed a low-Se, low-vitamin E basal diet (Marin-Guzman et al., 2000). Vitamin E supplementation had no effect on testicular sperm reserves, but Se supplementation significantly increased the number of Sertoli cells, secondary spermatocytes, and round spermatids.

Se in excess also affects reproduction, and reduced hatchability and deformed embryos have been seen in aquatic birds when concentrations (wet basis) of Se as selenomethionine in the egg exceeded 3 ppm (Spallholz and Hoffman, 2002).

Vitamin A

Vitamin A has been shown to play a fundamental role in vision, growth, and cellular differentiation. Retinol and its principal biologically active derivative, retinoic acid, also have been shown to be involved in regulation of testicular functions in rodents. Excesses lead to testicular lesions, spermatogenic disorders, and teratogenicity in rats and mice (National Research Council, 1995). Deficiencies result in early cessation of spermatogenesis and impaired testosterone secretion. Mice mutant for retinoic acid α receptors and retinoid \times β receptors are sterile. Retinoids appear to affect the metabolism or activity of the three main testicular cell types, Sertoli, germinal, and Leydig cells. Retinoids also appear necessary for proliferation and differentiation of A spermatagonia and for spermiogenesis. Decreased testosterone production associated with vitamin A deficiency leads to atrophy of the accessory sex glands (Livera et al., 2002).

Vitamin E and Vitamin C

The effects of vitamin E deficiency on development of the rat testis and epididymis were studied by feeding a vitamin E-deficient diet to lactating females starting on postnatal Day 10, weaning the young on Day 21, and continuing them on the deficient diet to Day 42 or 48. At these times, the young rats were killed and their tissues examined by light- or electron-microscopy for comparison with vitamin E-fed controls. At 42 days, testes were normal in appearance and had a full complement of germ cells. However, at 48 days, major abnormalities were evident, with incomplete spermatogenesis—the most advanced cell type being predominantly Step-7 spermatids. These and earlier spermatids were undergoing degeneration, with large pale areas in their nuclei, disrupted acrosomes, and uncharacteristic organelles in their cytoplasm. Lipid droplets were present in Sertoli cells, apparently representing breakdown products of the late spermatids that had been phagocytized. In the epididymis, poorly developed secretory and endocytic apparatuses were evident in the principal, narrow, and apical cells. These relatively short-term deficiency signs could be reversed by vitamin E supplementation, but it appears that vitamin E plays

an important role in maintaining spermatid viability and allowing full differentiation of epididymal epithelial cells (Bensoussan et al., 1998).

Studies have been conducted on the effects of dietary α -tocopheryl acetate (50 vs. 200 mg/kg diet) or ascorbic acid (0 vs. 1 g/L drinking water) on semen vitamin E concentrations and motion characteristics, oxidative stability, and fertilizing ability of rabbit spermatozoa stored at 5°C for 24 hours (Castellini et al., 2000). The higher dietary vitamin E level increased semen vitamin E concentration, and oxidative stability was improved. Vitamin C supplementation alone did not increase semen vitamin E concentration nor improve oxidative stability. The combination of the two vitamins significantly improved the viability and kinetics of spermatozoa and increased fertility rate (70.0 vs. 63.3%) to near significance ($P = 0.06$).

Ascorbic acid appears to be involved at several points in the reproduction of teleost fishes. Although much more research on function is needed, it appears to inhibit oxidative damage of the DNA in spermatozoa and ova both before and after spawning. Ascorbic acid also may be protective of the tissues of reproducing fish in the presence of enhanced UV-radiation or conditions of intensive aquaculture such as hypoxia, oxygen supersaturation, or intake of dietary prooxidants (Dabrowski and Ciereszko, 2001).

Calcium, Phosphorus, and Vitamin D

A possible direct effect of vitamin D on female reproduction has been investigated using vitamin D receptor-null mutant mice as a research model (Johnson and DeLuca, 2001). Infertility in these mutant mice had been reported, but it was not clear whether the defect was a consequence of the missing vitamin D receptor or from the associated hypocalcemia or hypophosphatemia. When fed purified diets ranging from 0.02–2.0% calcium (Ca), mutant mice consuming 0.47% Ca or less had lower reproductive efficiency than mutant mice receiving diets that maintained normal serum Ca concentrations. Normal mice fed diets containing 20% lactose, 2% Ca, and 1.2% phosphorus (P) without vitamin D had normal serum Ca and P concentrations and normal reproductive efficiency comparable to normal mice fed 0.47% Ca and 0.3% P with or without vitamin D (Johnson and DeLuca, 2002). It appears that the previously reported reproductive defect was not a direct effect of 1,25-dihydroxycholecalciferol on reproductive function but was a consequence of hypocalcemia and/or hypophosphatemia.

The Ca demands of egg production have been reported to induce many small passerines to forage intensively for Ca-rich foods during egg laying. The increased incidence of shell defects among wild passerines in Western Europe has been proposed as due to decreased Ca availability in soils because of acid deposition from long-term anthropogenic activity. Provision of Ca supplements in areas of low Ca availability has shown some promise. When captive zebra finches (*Taeniopygia guttata*) were switched from ad libitum Ca to low Ca and back again over the laying of three clutches, clutch sizes did not differ between these birds and ad libitum Ca control birds. Ca-limited birds took over 3 days longer to lay clutch three than did controls, but the difference was not statistically significant. However, birds on low Ca laid eggs that declined in shell ash mass with laying sequence and appeared to be Ca-limited (Reynolds, 2001).

CONCLUSIONS

As is so commonly the case with information on nondomestic species, published research on nutrition and reproduction either with captive or free-ranging wild animals is very sparse. Consequently, it has been necessary to examine studies with domestic animals and laboratory rodents for evidence of relations between nutrition and reproduction with potential importance for the welfare of wild species. This comparative approach has worked well for other periods of the life cycle, and it seems appropriate for reproduction, also. Indeed, considering the genomic evidence for similarities among widely divergent animal species, it is not surprising that some of the nutrients shown to be so important for reproduction of mammals, birds, reptiles, amphibians, and fish are important for insects, as well (Demott, 1998; Richards and Evans, 1998; Uchida, 1998). It is clear not only that there are nutrient deficiencies or excesses that directly impact reproductive events in subjects experiencing these deficiencies or excesses, but also that their consequences can impact the reproductive success of future generations. This is particularly important to understand if we hope to ensure the health and survival of wild animals in our care.

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