ARE SUPER-DOSE CONCENTRATIONS OF VITAMIN E REALLY NECESSARY FOR REPRODUCTION IN BIRDS?

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Abstract

Vitamin E requirements for exotic avian species remain undetermined and await investigation. As a result, diets formulated for captive exotic birds rely on the development of target ranges and feeding guidelines in order to minimize the risk of developing deficiencies and/or toxicities. These target ranges are commonly based on the requirements of domestic poultry, with the addition of calculation factors assumed to provide dietary concentrations at safe levels. It would be generally accepted, by many avian specialists, that these target ranges have reduced the incidence of vitamin E-induced pathogenesis in most species, especially in the past ten years. Nevertheless, considering the recommendations are often ten-times the requirements of domestic poultry, are the current supplementation practices significantly overemphasizing the actual dietary requirement? And if so, does it make physiological and metabolic sense to maintain offering dietary concentrations higher than probable requirements based on historical 'best-practices' and presumed reproductive gain?

Estimated Nutritional Requirements

The target ranges and estimated nutritional requirements for almost all exotic avian species have historically been calculated using the nutritional requirements of domestic species.[14] It has been well argued that the domestic granivorous bird are inappropriate models for most exotic species,[10] however they remain the only avian group in which the vitamin E requirements have been conclusively determined.[26] Nevertheless, as a consequence of this limited database of information in the early to mid 1980s there were numerous publications discussing the incidence of clinical vitamin E deficiency in captive exotic piscivorous birds.[6,23,31] It could be hypothesized that due to the high concentrations of polyunsaturated fatty acids in their diets, piscivorous birds were the most at risk of hypovitaminosis E, which led to the increased incidence in these species. As a result, with additional supportive data from Geraci et al[12] who showed that vitamin E deficiencies in captive fish-eating animals could be negated by supplementing fish with 100IU of vitamin E, it is probable that the combination of this information gave rise to the recommendation that captive exotic bird species be offered diets containing between 100 and 250IU/kg of vitamin E per kilogram of diet offered (dry matter basis).[8] This range remains the suggested recommendation and from the general reduction in published cases detailing the incidence of hypovitaminosis E, there would be general agreement that these levels are appropriate for most captive exotic avian species, including piscivores,[7] carnivores,[1,5] faunivores,[14] and omnivores/granivores.[9,17,19]

The importance of Vitamin E in bird health and reproduction

The term vitamin E refers to the two groups of compounds; the tocopherols and the tocotrienols, which have antioxidant activity in cellular membranes.[20] The most biologically active form is α-tocopherol[4] and is the standard used when describing a birds' requirement.[14] Plants are the only natural source of vitamin E and the concentrations of vitamin E depend on the location, maturation, environment, and the type of plant material.[41] To ensure commercial diets provide the minimum requirements, diets are often supplemented with a synthetically produced ester form (commonly *all-RAC* -α-tocopherol acetate).[41] Consequently, captive bird diets contain a range of naturally occurring and synthetic tocopherols and tocotrienols.[35]

Although the specific mechanisms of vitamin E digestion and absorption have not been elucidated in birds, it is generally accepted that it follows similar pathways as those in mammals.[14] Vitamin E is digested by the micelle pathway and there does not appear to be any intestinal bio-discrimination between tocopherols or tocotrienol isomers.[42] However, once associated with the hepatic system preferential uptake of α-tocopherol appears to occur due to the presence of α-tocopherol binding protein.[41] Tissue α-tocopherol increases proportionately with dietary intake, and unlike most other vitamins, there appears to be no saturation point[43]. Increasing levels of dietary supplementation have been shown to greatly enhance the concentration of vitamin E in the egg[11,16,35,39], however there are a number of factors that are known to affect absorption efficiency, including species,[36,41] vitamin A,[27,34] types of unsaturated fatty acids,[14,41] and *in vivo* oxidation of vitamin E.[42]

The requirements for vitamin E are primarily related to the level of potential oxidative stress caused by the production of free-radicals during oxidation reactions.[3] Primarily, vitamin E facilitates the prevention of uncontrolled oxidative degradation of polyunsaturated fatty acids, which are incorporated into cellular membranes, thus preserving its structural and functional integrity.[4,41] This process is contingent on the fast recycling of oxidized vitamin E with other enzymes and antioxidants, but this fast recycling also results in small amounts of vitamin E protecting relatively large amounts of membrane lipid.[13]

Due to the high concentrations of unsaturated lipids[25,28] and the onset of pulmonary respiration,[35] vitamin E is essential for embryonic development and chick survival.[44] A review by Surai[41] identified a number of studies showing reduced hatchability and survival in chicks produced by hens consuming diets deficient in vitamin E. These deleterious effects were attributed to vitamin E's role as the major chain breaking antioxidant of the second level of peroxidative defense during embryogenesis[35]. This is achieved by the accumulation of high concentrations of vitamin E in the yolk-sac membrane and embryonic liver during the last trimester of development[32,37]. These high concentrations decrease rapidly during the first three-to-five days post hatch,[33] consequently an increased vitamin E reserve is believed to be beneficial for postnatal survival[39] but chicks hatching from eggs that are marginally deficient die soon after hatch.[14]

Vitamin E content of eggs

Notwithstanding the importance of vitamin E for embryonic development there are limited data on the egg yolk concentrations of domestic species and even less in exotic species.[41]

Nevertheless, from data collected in domestic species it is likely that there are three major factors that influence the vitamin E content of egg yolks. Firstly, as previously stated, there is a positive relationship between the maternal diet and egg yolk vitamin E concentrations.[33,41] Secondly, there is a positive relationship between vitamin E requirements and hatching conditions of the chicks, notably that eggs producing precocial chicks often contain more vitamin E than their altricial counterparts.[25] And finally, there are species-specific differences in vitamin E metabolism. This relationship was demonstrated in four commercially important domestic species fed diets containing similar levels of vitamin E. The researchers showed that domestic chickens were four-times more efficient at dietary-vitamin E-to-yolk accumulation than the turkey, duck, or goose, respectively.[33] These three factors make attempting to estimate the concentrations of vitamin E in the eggs of exotic species very difficult and probably impossible.

Although these factors make estimating the egg yolk compositions of exotic birds difficult, there were expectations that species that consume diets containing high concentrations of long chain unsaturated fatty acids, would produce eggs containing significantly higher quantities of vitamin E.[38,40] This hypothesis was supported when eggs were collected from free-ranging pelicans (*Pelecanus erythorhynchos*), gannets (*Morus bassanus*) and cormorants (*Phalacrocorax auritus*)[38] showing vitamin E concentrations more than three times higher than those observed in free-ranging and feral domestic granivores. However, when similar analyzes were conducted on eggs produced by free-ranging king penguins (*Aptenodytes patagonicus*),[40] emperor penguins (*Aptenodytes forsteri*),[30] and lesser black-backed gulls (*Larus fuscus*),[21] vitamin E concentrations were not considerably different to those observed in free-ranging gallinaceous species[35] (Table 1). The researchers suggested that these differences are probably reflections of the differences in phylogeny, prey items, and efficiency of absorption. However, since not all feral domestic species produce eggs containing higher egg yolk vitamin E concentrations than their captive counterparts, this may support an idea of a 'basal' requirement for vitamin E which still results in successful embryonic development. As a result, these data appear to indicate a "diminishing effect" of increasing dietary vitamin E with increasing reproductive success. Where although a small percentage increase in dietary vitamin E may be beneficial for reproductive success, the law of diminishing returns results in no additional improvement in production above physiological necessities.

These "diminishing effects" provide support for the proposition that the current recommendations (100-250IU/kg) overemphasize the actual vitamin E requirements. In recently published research[18], the α-tocopherol concentrations of eggs produced by captive Humboldt and African penguins to be between 175 and 353μg/g, offered diets containing between 90IU/kg and 120IU/kg of vitamin E. The results are considerably higher than the levels observed in free-ranging penguins and between one- and two-times higher than the concentrations seen in the pelecaniformes. Similar results were observed by Barton *et al* [2] who showed that birds-of-prey offered diets containing 200IU of supplemented vitamin E produced eggs containing approximately 300IU/kg of α-tocopherol. Although there is no data on the vitamin E concentrations of birds-of-prey, these high concentrations are higher than what has previously been published for free-ranging piscivorous birds, and hypothesized to be higher than what would be seen in free-ranging birds-of-prey. Additionally, when eggs were collected from free-ranging Attwater's prairie chickens (*Tympanuchus cupido attwateri*), these eggs contained approximately 20μg/g of α-tocopherol, whereas eggs produced by captive birds consuming

170IU/kg and 330IU/kg of dietary vitamin E, produced eggs containing 49.7µg/g and 89.9µg/g, respectively. Moreover, since research in domestic species demonstrates a correlation between dietary concentrations and egg yolk composition, these data would suggest a similar effect exists in captive exotic species.[18] The major limitation to these findings, were that the eggs from the free-ranging Attwater's prairie chickens came from a nest that had been abandoned and that no data is available for eggs from free-ranging African or Humboldt penguins.

Nevertheless, it has often been widely assumed that an increase in egg yolk vitamin E composition will result in a beneficial effect on reproduction success. However, in both of these studies[18] there was no statistical improvement in success, even at the highest dietary intakes. Historical reproductive success of the institutions holding Humboldt and African penguins, showed no positive correlations between dietary vitamin E or egg yolk vitamin E composition, and reproductive success. Additionally, fertility, hatchability, and post-hatch survival were not significantly improved by the additional supplementation of vitamin E in Attwater's prairie chicken. Furthermore, Attwater's prairie chickens offered 1,000IU prior to the onset of lay,[15] showed no significant increase in reproductive efficiency when compared to those birds offered diets containing 170IU/kg or 330IU/kg. These data are in agreement with the review by Surai[41] who showed no additional improvement in reproductive success when dietary vitamin E was at concentrations considerably higher than requirements in domestic species.

These results suggest that super-dose concentrations may not improve or increase reproductive output in birds held in captivity and although, at no time did the levels observed in our experiments produce any signs of hypervitaminosis E, is long-term exposure to high concentrations of vitamin E a cause for concern? Currently, there has been only one documented case of hypervitaminosis E in a captive exotic species,[24] and that was after short-term exposure to high dietary intakes between 100IU and 10,000IU/day. Nevertheless, are the high concentrations in the eggs produced by captive exotic birds indicative of excessive intake of dietary vitamin E, which result in the birds 'dumping' excess amounts into the eggs? Certainly, the current published data could not be used as evidence of this 'dumping' effect, and since there are no indications of adverse effects on health and reproduction, the current recommendations (100-250IU/kg) are still the most valid data. However, as the role of exotic animal nutritionists is to continuously strive to understand animal physiology and develop diets based on good scientific methodology these data provide considerable support to questioning of the current supplementation practices and recommendations.

In conclusion, the authors of this review do not have a 'one size, fits all' solution and it is difficult to justify the collection of eggs from free-ranging species to determine egg yolk composition, especially considering these data may be variable also. Nevertheless, it is the object of this review to question the current viewpoint and to advocate that changes to this philosophy should be examined. Notably, that simply because there have been no outward incidence of toxicity, does not necessarily mean that physiologically disproportionate concentrations of dietary vitamin E are completely harmless either.

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Table 1: Comparison between the α-tocopherol (vitamin E (VE)) concentrations of eggs produced by captive (C), feral (F), and wild (W) granivorous and piscivorous birds.

	Species	C, F, or W	Dietary VE (IU/kg)	Egg Composition (VE - ug/g)	Citation
Granivorous	Domestic Chicken	C	15	33.21	Surai[41]
		C	22	160	
		C	114	273.4	
		C	120	305.6	
		C	250	685.9	
	Duck	C	23.4	46.2	Surai[35]
	Duck	F		26.1	
	Goose	C	24.1	40	
	Goose	F		22.6 – 33.2	
	Canada Goose	W		83.1	
	Pheasant	F		49.3-85.9	Speake et al.[29]
	Turkey	C	33.9	38.0	Surai[35]
	Attwater's prairie chicken	C	170	49.7	McClements[18]
		C	330	89.9	
		W		20.16	
Piscivorous	Humboldt or African penguin	C	51.61	181.1	McClements[18]
		C	54.19	204.6	
		C	90.10	356.6	
		C	102.43	250. 0	
		C	109.57	267.7	
		C	112.57	171.5	
	Emperor penguin	W		78	Speake et al.[30]
	King penguin	W		136.4	Surai et al.[40]
	L-BB Gull	W		50.2 – 97.6	Nager et al.[22]
	Suka	W		85	Surai[35]
	Coot	W		201.6	Surai et al.[38]
	Gannet	W		217	
	Cormorant	W		294	
	Pelican	W		299	