Review

Nutritional considerations for captive Charadriiformes (shorebirds, gulls and alcids)

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Abstract

A progressive decline in Charadriiforme populations prioritizes appropriate life-stage nutrition for captive Charadriiformes as conservation efforts continue to develop. These species are opportunistic feeders on fish and aquatic invertebrates. Appropriate life-stage nutrition for captive Charadriiformes requires nutrient provision beyond simple piscivory. This review presents existing data on relevant dietary components (protein, fat, carotenoids, minerals and vitamins) and examines the importance of these components in life-stage nutrition (embryonic development, neonates (chicks), juveniles, adults, breeding, incubation and chick rearing). The issue of determining metabolic rates of captive Charadriiformes populations is briefly presented. Eight recommendations for the amelioration of diet deficiencies are outlined.

Keywords: Charadriiformes, Captive, Nutrition, Avian piscivore

Review Methodology: The material included in this review was primarily selected from peer-reviewed journals from multiple databases. These journal articles were selected by the information and data applicable to the nutrition of captive Charadriiformes. The emphasis is on current research, although dated journal articles were included if the article was the basis for current research and/or was one of few existing journal articles on a relevant topic.

Introduction

Charadriiformes include species from approximately 17 families and most of these species are primarily piscivores although some authors make a distinction between piscivore and microfaunivore [1]. Piscivore diets are fish-based and microfaunivores primarily eat aquatic invertebrates (worms, starfish, urchins, molluscs, krill and arthropods) although most are opportunistic and will eat fish and/or aquatic invertebrates. However, in captivity, various limitations in provisioning diets for Charadriiformes result in all the suborders (alcids, gulls and shorebirds) being fed fish diets or, in short, all are fed as piscivores. Comparatively, the diets of Charadriiforme piscivores and Charadriiforme microfaunivores provide similar dietary protein and energy. A difference, however, in the diet of microfaunivores is the degree of prey exoskeleton (chitin and calcified tissue) [1]. Chitin in wild Charadriiformes diets has a digestibility of 35–84% [2]. The calcified tissue, if digestible, would raise the ash (calcium) content of microfaunivores compared with piscivores.

The gastrointestinal tract (GIT) of adult Charadriiformes is flexible, depending on diet [1, 3]. For example, the size of the gizzard (muscular action for crushing shells) increases when a bird's diet contains food with a high ratio of shell to flesh [4–6]. In general, microfaunivores would have the largest gizzards [1] because of the high percentage of prey exoskeletons in their diet. The caeca of Charadriiformes can vary from vestigial to large [1] and those species eating primarily diets with low ratios of flesh to shell (e.g. microfaunivores) would have the largest caeca.

As opportunistic foragers, the flexibility in size and function of GITs is directly responsive to diet although there is some variation in digestive efficiency between and among species and diets [7–9]. Sprat (*Sprattus sprattus*), a fish species high in lipid, was retained in the gut longer in nine seabird species compared with less energy-dense fish species (lesser sandeel, *Ammodytes marinus*; whiting, *Merlangius merlangus*) [7]. Sprat also had the highest digestive efficiency when fed to lesser black-backed gulls (*Larus fuscus*) [8]. Northern fulmars (*Fulmarus glacialis*) consistently had the longer gut retention times compared with eight other North Atlantic seabird species eating the same diet [7]. Digestive efficiency may be reduced if birds must switch from their normal diet [8].

To date, most zoological institutions holding Charadriiformes use a standard recommended approach to diet formulation: feed at least three varieties of fish and supplement with thiamine and vitamin E. The 'whole fish', however, often lacks viscera because the fish is provided by sources providing human-quality fish. In the wild, viscera are the primary source of some nutrients for avian piscivores and avian microfaunivores [1, 10, 11]. Therefore, these recommendations may not be adequate for captive Charadriiformes. The recommendations also lack detailed feeding information because research does not exist to provide valid and reliable data. Many captive avian piscivores have high-quality diets based on these recommendations but, compared with the diets of wild avian piscivores and the nutritional pathology and breeding difficulties seen with captive avian piscivores, these birds may need an increase in the quality of their captive diets.

In addition to a lack of research on general captive Charadriiformes nutrition, there is a dearth of research relevant to seasonal dietary needs (e.g. moult) and life-stage nutrition (e.g. breeding or neonatal) [12]. There is current research on life-stage nutrition in some wild populations of Charadriiformes, but the information provided by these studies may not be directly applicable to captive Charadriiformes populations [13]. For example, captive populations are selected and bred for survival in controlled environments without variability in temperatures, food source and water source [6, 13]. Selection for survival in controlled environments may create subpopulations with metabolic requirements and nutrient needs that differ from wild species.

Life-stage nutrition of captive Charadriiformes is of particular importance as zoological institutions continue to expand their participation in conservation efforts. The priorities of captive maintenance and breeding of Charadriiformes will increase as wild populations decline. In Canada, there is a progressive decline in Charadriiformes populations [14–19]. For example, population studies in 2005 found a 73% decline in species (30 species) and none of these species had a significant population increase during the study [19]. As captive populations increase in importance, considerations for diet provision must go beyond simple piscivory. This review will present factors beyond piscivory that are relevant to diet formulation of captive Charadriiformes.

Piscivory

Piscivory refers to a diet primarily of fish but most Charadriiforme species are opportunistic foragers and will also eat aquatic invertebrates and human detritus [1, 20]. In addition, prey variety taken by avian piscivores may vary between and within species. For example, in Norwegian waters, the diet of common guillemots (*Uria aalge*) is 80% fish (capelin, herring and sandeels) but the diets of Brünnich's guillemots (*Uria lomvia*) and black guillemots (*Cepphus grylle*) are 60% fish and 40% invertebrates (polar cod, capelin, gadoid and sandeels, capelin, sculpin, respectively) [21]. In comparison, guillemot species in the North Atlantic are exclusive piscivores (young gadoids, herring, pilchard, sandeels and sprat) [22]. Yet again, when feeding chicks, adult guillemots (*Uria aalge* and *U. lomvia*) preferentially feed their chicks energy dense prey (capelin, *Mallotus villosus*) and eat less-digestible crustaceans (euphausiids, *Thysanoessa inermis*) [23].

The variety of fish fed on by wild species is not available when feeding captives. Even the current recommendations to feed at least three species (fin fish and aquatic invertebrates for complementary nutrients) and supplements [10, 24] can be difficult to attain because of decreases in wild fish populations and the rising costs of farmed fish products. In addition, assuring the quality of the fish that is fed to captive Charadriiformes may further limit availability of these products. For example, the nutrient value (and palatability) of fish may deteriorate if it has not been properly shipped, stored, thawed and fed. Even under the best of such conditions, proteins will become denatured, fats can become rancid and vitamins are destroyed [10, 11].

Dietary Components

In addition to providing a basic fish diet, the delivery of appropriate macro- and micronutrients must be ensured if captive Charadriiforme populations are to prosper. Immediately relevant to this review as potential sources of dietary deficiencies and excesses in captivity are protein (amino acids), lipids (fat), carotenoids, minerals and vitamins.

Dietary Protein

Bird feathers are primarily 90% beta-keratin [25] and the amino acid composition of the keratin varies depending on the parts of the feather [26]. During moults, the quality of dietary protein (amino acid balance, digestibility and quantity) increases in importance because there is an average loss of 25% of the protein mass of a bird at this time. The amino acids cysteine and methionine (sulphur amino acids) are important for developing new feathers and these amino acids are the limiting amino acid in marine fish [11]. The average feather mass of a bird is 4–8% of body mass [1, 27]: therefore dietary protein is an important component of most avian diets (wild or captive). Birds in captivity moult seasonally in patterns similar to wild birds [28, 29]. In general, existing research on moulting relies on adequate to excessive provisioning of food for feather growth and regrowth but it cannot recommend specific dietary components [1, 30].

Dietary Fat

Dietary fat is used as energy for avians and fat averages about 2% of the diet dry matter (DM) [1]. The lipids supplied by fish are unsaturated fats [1]. The high lipid content in the prey of Charadriiformes is about 90% digestible for these species [31]. Developing embryos, in addition, use yolk lipids to provide 90% of the energy the chick needs for growth and hatching [32]. The lipids found in fish carcasses are unsaturated [11] but vary depending on the environment and life stage of the fish. For example, oily fish (coldwater fish and marine fish) does vary in fat content depending on life stage [10, 11]. These species store fat in their muscle and the carcass fat content can vary from 1% (after spawning) to 20% (before spawning). Fish from freshwater or warmer bodies of water store their fat in their liver (non-oily) [1, 10]. As previously stated, the fish carcasses fed to captive avian piscivores are often farm-raised for human consumption, lack viscera and the captive diet could be deficient in fat and fatty acids.

In addition to providing overall dietary fat requirements, there must be consideration for the types of fat and fatty acids inherent in dietary fat requirements. Linoleic (C18 : 2; 9,12-octadecadienoic acid) and alpha-linolenic (C18 : 3; 9,12,15-octadecatrienoic acid) are essential fatty acids for avians and probably also arachidonic acid (C20 : 4; 5,8,11,14-eicosatetraenoic acid) [1]. Fish carcasses vary in fatty acid content. For example, freshwater fish contains twice as much capric acid (C10 : 0; decanoic acid) and C18 fatty acids but less than half the quantity of C20 : 4 and one-seventh the quantity of behenic acid (C22 : 0; docosanoic acid) fatty acids than marine fish [11]. Squid is high in caproic acid (C6 : 0; hexanoic acid) as much as two to four times higher relative to other prey items [11]. Timnodonic acid (C20 : 5; 5,8,11,14,17-eicosapentaenoic acid – EPA) and docosahexaenoic acid (C22 : 6; 4,7,10,13,16,19-docosahexaenoic acid – DHA) is high in krill and herring. This data infers that the dietary fatty acid composition fed to freshwater avian piscivores possibly should differ than that fed to marine piscivores.

Another nutrition issue of captive Charadriiforme birds is the role of dietary fats needed for proper function of the uropygial gland (preen gland). This bilobed gland is a large gland in Charadriiformes [33] and can produce about 600 milligram (mg) of sebum [34]. The primary role of the preen gland is lipogenesis [1, 25, 35]. The preen gland secretes sebum made of monoester and diester waxes (composed of fatty acids, mucins, lipids and glycerides [1, 25, 35–37]). Sebum is smeared on feathers and podotheca by the bird using its bill and the coating maintains feather pliability and waterproofing [38]. In addition, the sebum has a pheromonal role [39–42], protects against ultraviolet (UV) light [43] and, it has an antibacterial and anti-mycotic role [25, 44]. The sebum produced by preen glands does vary among avian species [44] which is expected if it has a role in pheromone production, but it may not be directly linked to dietary fats. Fatty acids, for example, in the sebum of rock doves (*Columba livia*) include oleic acid, linoleic acid, arachidonic acid and palmitic acid but only four of the fatty acids were found in the birds' diet [45, 46]. Of the fatty acids in the sebum of rock doves, 58% were unsaturated fatty acids. Sebum also varies seasonally [34, 44]. Diesters, for example, appear in the sebum of wild birds only during breeding and incubation [47] and this change in sebum composition is also seen in captive birds. The mass of uropygial glands also varies dependent on the size and sex of the individual bird in Laridae (gulls, terns and skimmers) [34, 44].

Carotenoids

Dietary carotenoids are a source of pigmentation for Charadriiformes through absorption by fat globules in contour feathers. Dietary carotenoids are also precursors of vitamin A. In addition to pigmentation and vitamin A synthesis, carotenoids act as an antioxidant and have a protective role from UV light [1, 27]. Approximately 2% dietary fat (as an energy source) is needed by avians to facilitate the absorption of fat-soluble vitamins and carotenoids [1].

Charadriiforme species obtain their dietary carotenoids from their prey. Captives, however, may not get sufficient dietary carotenoids if they are fed whole fish without viscera or if they are not fed crustaceans. Fish prey (vertebrates) and crustacean prey (invertebrates) use carotenoids for embryogenesis, development and reproduction but crustaceans have higher levels [48]. There are several commercial products that could provide dietary carotenoids to captive Charadriiformes (e.g. astaxanthin, and canthaxanthin, crustacean meal) but, the bioactivity of these sources are easily degraded by light, heat, oxygen, enzymes and inappropriate pH environments.

Minerals

Research on the dietary mineral needs of Charadriiformes is nonexistent. In general, because recommendations specify feeding whole fish [10, 11], we assume (and we can only assume because of the lack of research evidence) that the calcium and phosphorous needs of captives are met.

Currently, identifiable mineral deficiencies and excesses for captive Charadriiforme species are related to dietary calcium deficits. Despite whole-fish diets (less viscera), the calcium deficits usually result because of a high dietary phosphorous level [10, 11] caused by inappropriate dietary supplementation. In addition, dietary levels of vitamin D_3 must be sufficient to support calcium metabolism yet not in excessive amounts to cause the development of a hypervitaminosis D.

We also assume that trace minerals exist in adequate amounts in captive Charadriiforme diets. The recent development of farmed fish, however, requires that we make distinctions between available nutrient levels in wild fish versus farmed fish [11]. Given worldwide water pollution levels, we also know that wild fish (some farmed fish also) may also have levels of metals, pesticides and other contaminants that could prove toxic to captive animals.

Dietary Vitamins

Whole fish can be an excellent source of dietary vitamins including vitamin D_3, vitamin A, riboflavin, niacin, pantothenic acid, vitamin B_6, vitamin B_{12} and choline. However, most of these vitamins are found in viscera [1, 10, 11]. If captive Charadriiformes are fed human-quality fish, they are eating carcasses with the viscera removed and may develop deficiencies. Supplementation is always an option when deficiencies are identified [49]. Again, however, we have the dilemma of providing a nutrient when we do not know the required dietary level.

The most likely toxicities that could develop from inappropriate supplementation are from the fat-soluble vitamins such as vitamins A, C, D and E. Many zoos and aquariums use nutritional supplements for piscivorous animals that contain vitamins A and D [11] even when feeding fish species with appreciable levels of these vitamins. Vitamin E is often prescribed if only because we know wild diets contain high levels and this vitamin is not stable during processing and storage to the point that bioactivity is significantly decreased or nonexistent [1, 10, 11, 50]. Vitamin C can be found in viscera [1] but deficiencies are probably likely in gutted carcasses. Supplementing thiamin (B_1) is a necessity when fish (clams, herring, smelt and mackerel) containing thiaminase (enzymatic decomposition of carcass thiamine) are fed [11, 50]. In addition, thiamine is degraded by heat and oxygen.

Life-stage Nutrition

Multiple Charadriiforme species are often housed together in captivity. Group feeding for these Charadriiformes is generally practiced in most zoological institutions. Feeding stations are provided throughout the exhibit and the group divides itself among these feeding stations. The exception is water and/or filter feeders and these species are fed by placing the food in the exhibit water. Feeding in this manner means all species and all life stages eat the same diet. The following examples for neonates, juveniles, adults and breeding will illustrate that such a diet and methodology is probably inadequate.

The increase in maintaining captive colonies for breeding during conservation programmes (including release programmes) requires providing the appropriate nutrition at the appropriate life stage. The need to provide appropriate dietary nutrients to embryos, neonates (chicks), juveniles and adults (maintenance and breeding) increases the complexity of captive Charadriiforme nutrition.

Embryonic Development

Most captive breeding programmes of Charadriiforme species have low success rates because of problems related to the development of embryos [32]. Research does exist on the nutritional needs of these embryos and – to date – lack of development is attributed to the fatty acid profiles in the yolk. This research indicates that the polyunsaturated fatty acid (PUFA) profiles of the egg yolks lain by captive birds is not the same as those of wild birds and, this difference has been linked to dietary differences between captive and wild birds [51, 52]. In addition, adult birds must have the appropriate dietary levels of vitamins A, D, E and carotenoids for successful embryonic development [53, 54].

Neonates

The successful growth and development of chicks raised in captivity is directly related to the parents' diet [11]. As stated in previous sections, there are difficulties in providing an appropriate diet to captive Charadriiforme species, therefore, it is probable that neonates may not receive food from the parents sufficient to meet their nutrient needs. For example, wild Charadriiforme adults feed their chicks a wide variety of prey and this variety is difficult to obtain for captives. Wild royal terns fed their chicks a minimum of seven prey species: anchovies, herring, jacks, mackerels, drums, porgies and mullets [55]. Parents also varied the size of prey brought to the chicks: small prey was fed posthatching and progressively larger prey was fed as the chicks developed. [55–58]. It may also be difficult for captive adults to meet the energy needs of their chicks in captivity because of institution group-feeding policies. Wild sandpiper chicks, for example, had a daily 5285 kJ (1263 kilocalories or calories) for the first 18 days post-hatching [6] and this energy requirement could increase to three times the amount by fledging [59].

Group-feeding policies may make it difficult to ensure that captive parents can obtain sufficient food for their chicks.

Juvenile

The juveniles of many Charadriiforme species require energy and nutrient levels different from adults of their species [12] but we lack research evidence as to what those levels may be. It may also be difficult to provide the appropriate prey for juveniles. Juveniles in wild populations of curlew sandpipers (*Calidris ferruginea*), crab plovers (*Dromas ardeola*) and Eurasian oystercatchers (*Haematopus ostralegus*), for example, have feeding specialties. These include specializing in smaller prey (curlew sandpipers and oystercatchers) and worm-feeding (oystercatchers) [12, 60]. Reasons for these specializations could include the smaller body size of juveniles, shorter bills, lack of foraging skills and adult (dominant) bird exclusion [12, 60, 61].

Adult

Evidence from research on wild Charadriiformes indicates that some captives also should have specialized diets according to their sex. The sexual dimorphism of many Charadriiforme species includes differences in body size and bill size and length that create diet specializations. For example, females of the ruddy turnstone (*Arenaria interpres*) are larger than the males and are more likely to have the ability to turn stones when hunting for prey [62]. Bill size and length dictates the type of prey a bird will successfully catch and eat. For example, male oystercatchers (short and thick bills) specialize in hard-shell prey and females (long and thin bills) in worm feeding [12, 63]. Males of the Eurasian curlew (*Numenius arquata*) specialize in worms and the females in clams because the latter have the longer, larger bill [4]. An exception exists in curlews: the female bristle-thighed curlew (*Numenius tahitiensis*) is bigger than the male but has a smaller bill [64]. One species of phalarope (red-necked phalaropes *Phalaropus lobatus*) is not sexually dimorphic and both the male and female eat the same diet [64]. The other two species of phalarope are sexually dimorphic: males have the smaller bill and they hunt from the surface water whereas females, with the larger bill, hunt deeper in the water.

Breeding, Incubation and Chick rearing

Some research evidence does exist to support the need for changes in captive Charadriiforme diets to prepare the adults for breeding [12]. This generally requires increasing the amount per feeding, increasing the frequency of feedings and, feeding *ad libitum* [1, 11, 65]. In general, increasing the quantity of food for the breeding birds is thought to sufficiently increase all nutrients to the appropriate levels. The appropriate prey for adult birds is also important for breeding, egg formation, chick hatching and chick growth [66]. The research, however, has not yet produced enough specific data on the nutrients and nutrient levels for successful captive breeding diets.

Energy needs for the incubating Charadriiforme parent depends on the species. Some species have a low basal metabolic rate (BMR) increase of 0.8% and other species use more than twice their BMR [67, 68]. For wild Charadriiforme parents, this range in BMR is because of the time and distance needed to forage when as much as 68% of energy expenditure may be needed for foraging [56, 69]. Captive birds do not need to forage long distances so much of this data is not applicable to captive diet formulation.

The pre-breeding moult and growth of new feathers after breeding also requires an energy increase (>40% BMR) and specific dietary nutrients [28]. Feathers are primarily keratin (inert after synthesis) and feather condition directly results from the bird's diet at the time of growth [27, 29, 30]. The amino acids cysteine and methionine (sulphur amino acids) are important for developing new feathers and these amino acids are the limiting amino acid in marine fish [11]. Research indicates that captive birds moult seasonally and they also have a decrease of about 25% in body mass similar to moulting wild birds [29]. The loss in body mass in captive birds during moult occurred despite *ad libitum* feeding [28] and is attributed to an increase in BMR, increased nutrient demand, increased amino acid metabolism and increased heat loss.

Metabolic Rates

Specifically, we do not know if the BMR of captive Charadriiformes differ from wild birds. In general, however, the BMR of female birds correlates with spleen mass and the BMR of male birds correlates with intestinal tract and lung mass [1]. If the breeding of captive populations (in controlled environments without variability in temperatures, food source and water sources) does result in sub-populations [6, 13], it is possible that visceral masses may differ between wild and captive Charadriiformes populations. As a result, all measures of metabolic rates may differ. Variation in the size of visceral organs has been found to be specific to geographic location as a proximate factor in metabolic rate [70], therefore – using any captive zoological population as a geographical location – it may be assumed that metabolic rates differ between wild and captive Charadriiformes populations.

In addition, probable body mass differences between captive and wild Charadriiformes would also result in differences in BMR between these populations. A larger body mass, generally, means a lower BMR [71]. Captive birds would most likely have higher body masses because of reliable food sources, inactivity and controlled environments.

Conclusion

This review on issues relevant to the nutrition of captive Charadriiforme species indicates that the data is lacking to appropriately formulate diets for all life stages of these birds. In general, captive piscivorous birds are fed basic diets and supplements that – according to this review – may not be providing appropriate and sufficient nutrition. Amelioration of this situation may require:

1. Investigation of possible differences in physiology relevant to the nutrition and breeding of captives by comparing diets of captive populations with their wild counterparts.
2. Investigation of fatty acid and amino acid constituents of prey and offering complementary prey species. For example, nutrient differences between 'oily' fish and 'non-oily' fish and the nutrient status of wild birds (wide variety of prey) and captive birds (limited prey variety).
3. Investigation into the specific indices needed to provide captive piscivorous birds with the appropriate diets and/or supplements especially are: amino and fatty acid spectrums. Such an investigation should consider differences in dietary fatty acid composition that may exist between freshwater and marine Charadriiformes. In addition, investigation is needed to provide data on the dietary fatty acids required for optimum function of the uropygial gland. Included in these investigations should be provisioning of diets to optimize the breeding success of conservation programmes by providing the correct PUFA profiles of the egg yolks for captive birds and the appropriate dietary levels of vitamins A, D, E and carotenoids for successful embryonic development.
4. Investigation into provision of the correct supplementation needed to substitute for the lack of viscera in the diets of captive piscivorous birds. Fish viscera are important sources of fat, carotenoids, minerals and vitamins. Supplementation without research data may put captive populations at risk for further nutritional pathology and reproductive failure. In addition, the availability or development of nutritional supplements without the fat-soluble vitamins A and D should be investigated. We do know how to identify calcium excesses and deficiencies but, usually, it is identified by medical diagnosis and the condition is treated like a disease. A major problem in providing appropriate dietary mineral levels to captive Charadriiformes is the lack of reliable and valid research data. At the present time, we do not know of other mineral deficiencies or excesses because we do not know the appropriate dietary levels.
5. Investigation into differences of nutrient composition between wild and farmed fish including deleterious substances such as metals and pesticides.
6. Investigation into the diet differences of juvenile Charadriiformes to ensure the development of these birds into healthy adults with successful reproductive futures.
7. Investigation into the provision of appropriate diets for adult birds including sexual dimorphic variations; energy and nutrient provision for pre-breeding moult; and, energy and nutrient provision for optimum feather growth.
8. Investigation into the appropriate metabolic status of captive birds at all life stages for successful energy provision.

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