



Composition of fat and the effect on migratory flight in birds

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Abstract:

Fat, which is a prime source of energy for migratory birds, has been focused by various researches on the relevance of fat stores composition to flying performance. Dietary fat composition influences bird's ability to flight performance during migration. Experiments on food selection and seasonal variations in adipose composition have not yet shown conclusive proof that fatty acid content can alter flight performance. Nonetheless, it has been shown that direct dietary fat alterations can affect exercise capacity in both avian and non-avian species. There is mounting evidence that fatty acids with shorter chains or more double bonds perform at their peak levels longer because of faster transit rates to oxidation. Flight efficiency and endurance may or may not be affected similarly.

Keywords: Fat, migratory, triacylglycerol, flight, composition

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325

1. Introduction

In contrast to other macromolecules (carbohydrate and protein), migratory animals across a wide range of evolutionary lineages tend to store fat as the energy source to fuel their long-distance migrations (Blem, 1980; Dingle, 1996). Fat is much more energy dense than carbohydrate or protein, making it useful for reducing weight during long-distance movement even though it is more difficult to transport through aqueous media like cytosol or plasma (Alerstam, 1993; Blem, 1980; Klasing, 1998; McWilliams *et al.*, 2004; Ramenofsky, 1990). Flying animals, such as birds, are under particularly strong selection pressure to utilise stored fat to reduce weight during migration (Jenni and Jenni-Eiermann, 1998; Pennycuik, 1989) because of the enormous energy expenditure to fuel their long-distance flight (Pennycuik, 1972). Moreover, fat converts food energy more effectively than protein, thus maintaining adipose tissue is less expensive than maintaining protein reserves (Klasing, 1998). In fact, long-distance flights in migratory birds are predominantly powered by fat (Jenni and Jenni-Eiermann, 1998; McWilliams *et al.*, 2004). But little is understood about how various forms of fat affect these flights.

2. Fatty acids type and nomenclature

Fatty acids consist of a carboxylic acid group with a long aliphatic carbon chain. Vertebrates typically utilize unbranched fatty acids with chains between 12 and 24 carbons as source of energy (Raclot, 2003). Unsaturated fatty acids have at least one double bond between two carbon atoms, while saturated fatty acids have all of their carbon atoms joined by single bonds. Standard nomenclature, which identifies them starting from the carboxylic end of the molecule, can be used to denote the location of the double bond. Thus, the fatty acid that goes by the name linoleic acid is actually called *cis,cis- Δ^9 , Δ^{12} -octadecadienoic acid*. This fatty acid has 18 carbons, with double bonds at the 9th and 12th carbons from the carboxyl end. However, this notation is cumbersome because natural fatty acids almost always have double bonds that are precisely three carbons apart and because, more importantly, fatty acids are modified by enzymes close to the carboxyl end. As a result, this notation makes it difficult to distinguish between fatty acids that are related to one another enzymatically (Price, 2010). Hence, the position of merely the first double bond from the methyl end of the molecule is indicated by a conventional " ω " notation (Holman



and Mohrhauer, 1963). Hence, linoleic acid can be represented as 18:2 ω 6 (also written as 18:2n6 or 18:2n-6), showing that it has 18 carbons, two carbon-carbon double bonds, the first of which occurs at the carbon 6 from the methyl end, and is composed of two carbons. Moreover, it is clear that 18:2 ω 6 and 20:4 ω 6 are connected by two phases of enzymatic desaturation and one step of elongation (Price, 2010).

Fatty acids with two or more carbon-carbon double bonds are known as polyunsaturated fatty acids (PUFA). They typically exist as ω 3 or ω 6, fatty acids. Although they can be altered by desaturation and elongation, birds are unable to synthesize de novo the ω 3 and ω 6 fatty acids (Stevens, 1996). The ω 6 fatty acids are important nutrients required for some specific cell functions (Stevens, 1996). The ω 3 fatty acids are crucial for mammals and may also be essential nutrients for birds (Watkins, 1991). Because they are essential, ω 3 and ω 6 PUFA can have a significant effect on a variety of physiological processes (Watkins, 1991). Triacylglycerol (also known as "triglyceride"), which is made up of three fatty acids esterified to a glycerol backbone, is the storage form of fatty acids. The majority of triacylglycerol is found in muscles and adipose tissue. Common phospholipids share similar structure with triacylglycerol, with the exception that one of the fatty acids has been replaced with a head group that contains phosphate. Major parts of cellular and subcellular membranes are phospholipids (Price, 2010).

3. Absorption of fatty acids from food

It is possible for dietary fatty acids to be incorporated to the body tissues intact (Klasing, 1998). Furthermore, dietary fats have the potential to influence a variety of physiological processes because they are known to alter the composition of a wide range of bird tissues, including eicosanoids and muscle membranes (Klasing, 1998; McCue *et al.*, 2009; Thilet *et al.*, 2003; Watkins, 1991; Xuet *et al.*, 1994). Dietary triacylglycerol is hydrolyzed to create monoacylglycerol and non-esterified fatty acids (NEFA) in the intestine, which are then absorbed in the epithelium of the intestine (Denbow, 2000; Leeson and Summers, 2001; Place, 1996; Ramenofsky, 1990). These substances are reesterified to triacylglycerol before being transported to the liver and other tissues as portomicrons (similar to mammalian chylomicrons) through the venous portal system (Bensadoun and Rothfield, 1972; Ramenofsky, 1990; Stevens, 1996). To be circulated to different tissues, fatty acids may be altered in the liver and subsequently repackaged

as triacylglycerol in very low-density lipoproteins (VLDL) (Klasing, 1998; Stevens, 1996). As triacylglycerols from portomicrons or VLDL enter tissues like adipose or muscle, lipoprotein lipases hydrolyze them to create free fatty acids that are then transferred into those tissues where they can be reesterified to generate triacylglycerol (Ramenofsky, 1990). As a result, dietary fatty acids may be completely absorbed into intramuscular and adipose triacylglycerol. Prior to being stored in muscle or adipose triacylglycerol, dietary fatty acids may also be modified by enzymes through elongation and desaturation. De novo synthesis of fatty acids from protein or carbohydrate substrates also takes place in liver, primarily resulting in the generation of the 16:0, 16:1 ω 7, 18:0, and 18:1 ω 9 fatty acids. Thus, the total fat content of the diet will be crucial in determining the composition of adipose fat. Low-fat diets will cause the storage of significant amounts of these four synthesizable fatty acids, whereas high-fat diets will produce adipose tissue that is more similar to the dietary fatty acid composition (Griminger, 1986; Hudgins, 2000; Nelson, 1992; Williams and Buck, 2010). Overall, the makeup of tissue triacylglycerols will be influenced by dietary fat composition, the effectiveness of absorption of dietary fatty acids (Pierce *et al.*, 2004), post-absorptive modification of those dietary fatty acids, de novo synthesis, and possibly other processes like preferential mobilisation (Price *et al.*, 2008; Raclot, 2003) and preferential oxidation of specific fatty acids by muscles (Price, 2009).

Although birds can oxidize intramuscular triacylglycerol for energy, extramuscular lipid reserves are needed for prolonged flight (Jenni and Jenni-Eiermann, 1998). Hormone sensitive lipase and other lipases hydrolyze adipose triacylglycerol, releasing fatty acids into the bloodstream (Ramenofsky, 1990). Fatty acids bind to circulating albumin, where they are then delivered to muscle. Before reaching the muscles, certain fatty acids may be redirected to the liver and packed in triacylglycerol in VLDL (Jenni-Eiermann and Jenni, 1992; Landyset *et al.*, 2005). The translocation of fatty acids through muscle membranes is mediated by proteins (Luikenet *et al.*, 1999; McFarlanet *et al.*, 2009). Fatty acids are transported to the mitochondria within myocytes while attached to the cytosolic fatty acid binding protein H-FABP (Guglielmoet *et al.*, 1998). Acyl-CoA synthetase transforms fatty acids into acyl-CoAs, which are then transformed to acylcarnitines by the enzyme carnitinepalmitoyltransferase. A translocase is subsequently used to help the acylcarnitine cross the mitochondrial membrane.

Carnitinepalmitoyltransferase II then uses this newly generated acyl-CoA to perform β -oxidation, producing ATP. Before being transported to mitochondria for complete oxidation, fatty acids may also be partially catabolized in peroxisomes in a manner similar to mitochondrial β -oxidation (Berg *et al.*, 2002). NEFA and glycerol 3-phosphate are used to create phospholipids, which at first share the same anabolic route as triacylglycerols. Hence, dietary fat may potentially have an impact on the phospholipid composition. While some phospholipid classes, such as phosphatidyl inositol, have relatively constant fatty acid compositions, the composition of the fatty acids that make up the “tails” of most phospholipid classes can change significantly (Berg *et al.*, 2002).

4. Dietary lipid composition affects the efficiency of migratory flight

It is widely accepted that for birds to maintain normal growth and maintenance, their diets must contain a small amount of PUFA (Stevens, 1996; Watkins, 1991). There is evidence that the dietary lipid composition affects the efficiency of migratory flight. Above this fundamental level of nutrition, however, the consequences of food composition in vertebrates remain poorly known (McKenzie, 2001). Due to their potential to affect migratory flight performance, ornithologists have taken a special interest in the effects of dietary fatty acids (Pierce and McWilliams, 2005; Weber, 2009).

The content of stored fats and how that composition varies seasonally were observed previously in migratory birds (Blem, 1976, 1980; 1990; Pierce and McWilliams, 2005). Due to the idea that migrants should be more easily mobilised, this research has mainly concentrated on the percentage of unsaturates carried by migrants (Blem, 1976; Conway *et al.*, 1994; Johnson and West, 1973; Johnston, 1973). Blem (1980) came to the conclusion that there is no consistent difference between migrants and non-migrants with respect of lipid unsaturation in birds. Only a small number of species have had their fat composition examined in both migratory and non-migratory seasons (Pierce and McWilliams, 2005) and only about half of them show increases in unsaturation during the migratory period (Klaiman *et al.*, 2009; Pierce and McWilliams, 2005). Some researchers who used iodine value as a metric of unsaturation observed no seasonal variations (McGreal and Farner, 1956) or erratic variations linked to migratory fattening (Hicks, 1967; Nakamura, 1962, 1969). These sparse data do not provide compelling evidence for increases in unsaturation caused by migration.

Although, other processes like de novo synthesis and post-absorptive modification cannot be ignored, dietary lipid composition has a significant role on adipose fatty acid composition (Pierce and McWilliams, 2005; Egeler *et al.*, 2003; Klasing, 1998; Napolitano and Ackman, 1990; Pierce and McWilliams, 2005; West and Meng, 1968). This involvement of nutrition is significant because it might explain seasonal trends in fat composition (or lack thereof, if certain desired fatty acids are scarce). According to Bairlein and Gwinner (1994), birds have been found to occasionally change their diets while migrating, which may account for some of the seasonal patterns seen. Also, if the composition of stored lipids influences flight, birds may be able to enhance their flight performance by merely changing their diets. However, it is unclear whether these dietary changes are made to alter the composition of fat depots as some authors have proposed (Bairlein, 1996; Conway *et al.*, 1994; Heitmeyer and Fredrickson, 1990); or whether they are merely the result of birds adjusting to seasonal changes in food item abundance to maximise weight gain. Pierce and McWilliams (2005) have found no seasonal differences in preference for dietary fatty acids in their controlled studies with red-eyed vireos. Hence, diet changes may enhance overall migratory performance by boosting refuelling rate and survival at stopover, but there is limited proof that birds change their diets seasonally to obtain specific fatty acids that enhance exercise performance during flight (Price, 2010).

Seasonal variations in the ratio of monounsaturates (16:1+ 18:1) to 18:2 ω 6 in stored fat have previously been discussed (Blem, 1976; Pierce and McWilliams, 2005). However, the data are again few and ambiguous, with only 4 of 7 species demonstrating the pattern across seasons in the wild (Klaiman *et al.*, 2009; Pierce and McWilliams, 2005). Migrants have been assumed to carry higher quantities of monounsaturates compared to 18:2 ω 6. The basic character of 18:2 ω 6 in combination with the deposition of 16:1 and 18:1 offers one potential explanation for such a seasonal pattern. Since the fatty acids 16:1 and 18:1 can be formed from non-fat substrates or deposited directly from dietary sources, migratory hyperphagia in conjunction with an increase in the conversion of carbohydrates or protein to fat may be the driving force behind this pattern (Egeler and Williams, 2000; Napolitano and Ackman, 1990). Nevertheless, Pierce and McWilliams (2005) found no proof of a pattern of increasing ratio of (16:1+ 18:1)/18:2 ω 6 in adipose during the migratory season in a captive study of

red-eyed vireos under natural light conditions and controlled food.

The liver enzyme Δ^9 -desaturase that changes 18:0 to 18:1 in western sandpipers, has been increased during the migratory season in western sandpipers, *Calidrismauri* (Egeleret *al.*, 2000). This could, in part, be the cause of the rise in adipose depot unsaturation during the migratory period (Egeler and Williams, 2000), but it could also just be a result of the rise in de novo fatty acid synthesis generally observed during migration (Egeleret *al.*, 2000). Regardless of whether there is an increase in unsaturation during the migratory period, this study shows that some amount of unsaturation seems to be required in the deposition of adipose triacylglycerol. The adipocytes of semipalmated sandpipers (*Calidrispusilla*) during a stopover showed increases in the proportions of several polyunsaturates (20:5 ω 3 and 22:6 ω 3), according to Maillet and Weber (2006). This was linked to consuming prey that was substantially enriched in those fatty acids (Maillet and Weber, 2006).

Garden warblers (*Sylvia borin*) prefer to consume 18:1 to 18:0 and also prefer 18:1 to 18:2 ω 6, but this latter preference was not as strong as the former. This preference was demonstrated by Bairlein (1991) using pure triacylglycerols and natural oils. Similar research by McWilliams *et al.* (2002) revealed that yellow-rumped warblers (*Dendroica coronata*) prefer unsaturated free fatty acids over saturated ones, and that this preference is higher when 18:1 is the unsaturate used rather than 18:2 ω 6. Red-eyed vireos (*Vireo olivaceus*), likewise show preferences for 18:1 over 18:0, but there is no distinction in preference between 18:1 and 18:2 ω 6 (Pierce *et al.*, 2004). This research was expanded to demonstrate that, regardless of the time of year, vireos preferred 18:1 to saturated fatty acids (16:0 and 18:0) (Pierce and McWilliams, 2005). Differences in assimilation efficiency have been usually cited as the cause of this preference for 18:1, as 18:1 is simpler to absorb than its saturated counterpart 18:0 (McWilliams *et al.*, 2002; Pierce *et al.*, 2004; Place, 1996; Renner and Hill, 1961). Yet, migratory birds' preferences raise the idea that they may select dietary lipids that enhance migratory flying efficiency (Bairlein, 1996). Additionally, these preference studies have concentrated on the major components of bird adipose tissue (16:0, 18:0, 18:1 and 18:2 ω 6), but minor components (e.g., 15:0, 18:3, 20:0, 20:4 ω 6, 20:5 and 22:6 ω 3) have been proposed to play significant roles in influencing both whole-organism and cellular performance (Guderley *et al.*, 2008. Maillet and Weber (2006)

hypothesised that semipalmated sandpipers select foods that are richer in ω 3 fatty acids during stopovers.

Dietary fatty acids have been found to have an effect on whole-animal exercise performance in studies of non-avian species. Ayre and Hulbert (1997) showed that modifying the content of fats in the diet can affect endurance running in rats. They focused on various ratios of ω 6 to ω 3 fatty acids in their study. Maximum swimming speed of salmon was discovered to be influenced by the combination of oils present in their experimental meals, according to McKenzie *et al.* (1998). According to two studies done on birds (Pierce *et al.*, 2005; Price and Guglielmo, 2009), the lipid composition of the food can have an impact on the peak metabolic rate attained during exercise-wheel (burst performance) trials. Moreover, McWilliams and Pierce (2006) have found that the quantity of energy utilised during lengthy flights in a wind tunnel might be influenced by dietary fat composition.

Another study has shown that dietary ω 3 fatty acids are associated with increases in the activity of the muscle oxidative enzyme in semipalmated sandpipers during a migratory stopover (Maillet and Weber, 2006, 2007). However, it is not obvious if the ω 3 fatty acids present in the food or other migratory preparation activities at the stopover are responsible for the observed increases in oxidative ability. More subsequent research has shown that sedentary quails (*Colinus virginianus*) held at controlled dietary manipulation may induce these changes in enzyme activity (Nagahuediet *al.*, 2009). It is challenging to interpret these results in light of other studies (Ayre and Hulbert, 1997; McKenzie *et al.*, 1998; Price and Guglielmo, 2009) that demonstrate higher exercise performance with low levels of dietary ω 3 fatty acids in birds and other vertebrates (but see also Wagner *et al.*, 2004). Overall, these investigations show that dietary lipid composition alone can influence exercise performance in birds, although the exact mechanism underlying this impact is yet unknown.

Improved identification of the fatty acids that influence performance would be a worthwhile research direction. Ayre and Hulbert, 1996; Guglielmo *et al.*, 2002b; McKenzie *et al.*, 1998; Price and Guglielmo, 2009; have focused on ω 6 fatty acids. Maillet and Weber (2006); Nagahuediet *al.* (2009); Weber (2009) have focused on ω 3 fatty acids. Pierce *et al.*, (2005) have focused their study on total unsaturated fatty acids and McWilliams and Pierce (2006) have done their study on total polyunsaturated fatty acids. The best diet for

exercise may consist of an ideal mix of these components or others, and it may differ depending on the species and type of exercise. In this regard, the complexity of fat composition poses a significant experimental challenge because increasing the dietary proportion of one fatty acid or class of fatty acids will inevitably lead to a decrease in the proportion of other fatty acids, making it challenging to link changes in any one fatty acid or class to changes in exercise (if such changes are observed).

5. Flight-performance enhancing mechanisms

Early studies of migration-related increases in unsaturation gave rise to the theory that unsaturated fatty acids improve performance because they should be used more readily during exercise due to their higher solubility and diffusion rates in water (Blem, 1976; Conway *et al.*, 1994; Egeler and Williams, 2000; Johnson and West, 1973; Johnston, 1973). Unsaturated fatty acids should be transported through the body more rapidly and easily for future oxidation in the muscles of flight, possibly permitting faster rates of oxidation. The full fatty acid supply chain, including lipolysis and the release of fat from adipocytes, systemic transport, muscle absorption, intramyocyte transport, and finally intramyocyte oxidation for ATP production, is covered by this concept (Price, 2010).

There is strong evidence from other taxa that fatty acid type plays a significant influence in mobilisation and use (Egginton, 1996; Raclot and Groscolas, 1993). Different rates of whole-organism oxidation for a number of fatty acids administered to rats were shown by Leyton *et al.* in 1987. However, because birds consume lipids at higher rates than mammals and because migratory flight is primarily driven by fats mobilised from adipose tissue rather than the gut, their study may not be directly analogous to avian migratory flight. Similar to this, McCue *et al.* (2010) showed variations in the whole-organism oxidation rates of oral lipid doses in birds. Nevertheless, these variations in intestinal fatty acid absorption (Pierce *et al.*, 2004; Place, 1996) could also be the cause of these variations. The transport and utilization of stored fat have been studied at several steps along the lipid supply pathway in migratory birds: adipocyte lipolysis (Price *et al.*, 2008; Ramenofsky *et al.*, 1999; Vaillancourt and Weber, 2007), circulatory transport (George and John, 1993; Jenni-Eiermann and Jenni, 1992), muscular uptake (McFarlanet *et al.*, 2009; Ramenofsky *et al.*, 1999; Savard *et al.*, 1991), intramyocyte transport and oxidation (Driedzic *et al.*, 1993; Guglielmo *et al.*, 2002a; Lundgren and Kiessling, 1985; Marsh, 1981; McFarlanet *et al.*, 2009;

Pelserset *et al.*, 1999).

Researches that have examined the effects of various fatty acid types have typically demonstrated that fatty acid type has a significant role in influencing the rates of these activities. It has been demonstrated that regardless of migratory condition or recent activity, unsaturated and shorter chain fatty acids are preferentially mobilised *in vitro* from adipocytes in ruffs (*Philomachus pugnax*) and white-crowned sparrows (*Zonotrichia leucophrys*) (Price, 2009; Price *et al.*, 2008). This mechanism exhibits the same pattern *in vivo* as that seen in king penguins (*Aptenodytes patagonicus*) while fasting (Groscolas, 1990). Similar patterns of mobilisation are also seen in common pheasants (*Phasianus colchicus*) that are fasting (Mustonen *et al.*, 2009); the selective retention of some polyunsaturated fatty acids seen by Mustonen *et al.* (2009) appears to be an artifact of the presence of membrane phospholipids in their samples. Furthermore, it appears that the amount of fatty acid substrate supplied affects the rates at which fatty acids are transported into the mitochondria of avian muscle mediated by the enzyme carnitine palmitoyltransferase (Price, 2009).

It has been challenging to identify selective mobilisation or selective uptake *in vivo* during exercise, possibly because of the similarities in the pattern of preference for both adipose mobilisation and muscular uptake (shorter fatty acids and those with more double bonds have higher transport rates in both processes) (Price, 2010). Increased absorption of a specific fatty acid from plasma may counteract an increase in that fatty acid's mobilisation, maintaining the proportion of that fatty acid in plasma. According to Mougioset *et al.* (1995), exercise has a significant effect on the composition of plasma NEFAs in humans. This is because, most plasma fatty acids rise proportionately to their concentration in adipocytes. Vaillancourt and Weber (2007) observed no alteration in the plasma NEFA composition during shivering in ruffs. Vaillancourt and Weber (2007) came to the conclusion that there was no selective mobilisation of adipose fatty acids, though this finding could also point to similar selective mobilisation patterns in birds during rest and exercise, or to a close correlation between selective adipose mobilisation and selective muscular uptake. In the forearm muscles of working individuals, preferential absorption of 18:2 and 18:1 relative to 16:0 has been established (Hagenfeldt and Wahren, 1968).

Maximum flight performance in migratory



birds may be restricted by additional parameters like oxygen supply or oxidative capability (such as mitochondrial density) (Butler and Woakes, 1985; Jenni and Jenni-Eiermann, 1998; Marsh, 1981; Suarez, 1996; Weber, 1992). If this is the case, fatty acid selectivity through this route might not have any effect on peak performance. Citrate synthase (CS), an oxidative enzyme, also increases in abundance during migration (Driedzic *et al.*, 1993; Guglielmo *et al.*, 2002a; Lundgren and Kiessling, 1985; McFarlanet *et al.*, 2009), suggesting that either the availability of fatty acids or the ability of an organism to use their oxidative capacity could be a barrier to their ability to perform at their peak during migration. Moreover, oxygen availability has been seen as a barrier to aerobic performance in homeothermic vertebrates (Suarez, 1996), while migrating birds have not yet been fully studied in this regard (Jenni and JenniEiermann, 1998). Even when the supply of fatty acids is constrained, some supply pathway steps could be more crucial than others. Particularly, it is believed that the fatty acid supply pathway is constrained by circulatory transport, particularly muscle uptake (Guglielmo *et al.*, 2002a; Jenni-Eiermann and Jenni, 1992; McFarlanet *et al.*, 2009; Vocket *et al.*, 1996; Weber, 1992).

The question of whether metabolic limits are typically achieved during migratory flight is also crucial. Conway *et al.* (1994) pointed out that easily mobilised fat reserves might help migrants in unpredictably bad weather, probably because bad weather could drive migrants to approach maximal metabolic rates in order to fly in strong winds. Nonetheless, it's possible that birds don't always reach their peak metabolic rates while migrating. Instead, longer flights can be accomplished with the same amount of energy expended thanks to better endurance or energy efficiency. This is especially true for flights that traverse geographical borders, allowing for longer flights between stops. Given that unsaturated fatty acids are transported at higher rates than saturated fatty acids, one can imagine a mechanism by which birds using stored unsaturated fatty acids would use less energy to maintain the fatty acid transport proteins (such as H-FABP, fatty acid translocase, etc.), resulting in increased efficiency during flight. According to McWilliams and Pierce (2006), birds fed diets rich in polyunsaturated fatty acids used 13% less energy during 6-hour wind tunnel flights than birds fed diets rich in monounsaturated fatty acids.

In conclusion, researches support the idea that unsaturated and short-chain fatty acids

influence exercise through enhanced transport rates and thus greater supply to muscle mitochondria. Nonetheless, given the uncertainty surrounding the significance of peak metabolic rates during migration and in light of other suggested reasons of changed performance, this idea still merits additional investigation. We cannot conclude that migration causes an increase in the total level of adipose unsaturation of adipose stores. The storage of fat or the fueling of long-distance flight, however, may necessitate and/or benefit from a certain level of unsaturation. Nearly all dietary fat composition factors, as well as fat quantity, de novo synthesis, and the selective deposition, utilisation, and modification of dietary fatty acids, have an impact on seasonal changes in the fatty acid composition of adipose reserves.

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