Respiratory quotient: Effects of fatty acid composition

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Abstract

Respiratory quotient (RQ) is commonly used to infer which substrates are oxidized, with glucose yielding RQ = 1 and fat normally thought to yield an average of RQ = 0.71. Because fat depot compositions differ among species, we examined how the various common fatty acids affect RQ. RQs ranged from less than 0.7 (e.g., stearic acid) to greater than 0.76 (e.g., docosahexaenoic acid). Furthermore, we conducted a survey of the fatty acid composition of fuel lipids of several vertebrate taxa to determine how the RQ for lipid oxidation during fasting should vary among species. Our survey indicates that most fasting vertebrates from terrestrial ecosystems oxidizing fat should have RQs equaling approximately 0.71, as normally expected. However, some fasting animals in aquatic or marine systems—particularly fish—should have RQs as high as 0.73 when oxidizing only fat. Selective mobilization of fatty acids increased the lipid RQ, but probably by a negligible amount. We conclude that researchers should take habitat and taxon into account when choosing a value for lipid RQ, and preferably should use fatty acid composition for their study species to determine an appropriate RQ for lipids. In the absence of species-specific fatty acid composition data, we suggest assuming a lipid RQ of 0.725 for cold-water fish.

KEYWORDS

docosahexaenoic acid, fat composition, fish, fuel mixture, respiratory exchange ratio, respiratory quotient

1 | INTRODUCTION

The respiratory exchange ratio (RER), calculated as the volume of carbon dioxide (CO_2) produced by an animal divided by the oxygen (O_2) consumed, is commonly used as an indicator of the fuel being oxidized. It is often assumed to reflect the exchange ratio of gases at the cellular level (i.e., the respiratory quotient [RQ]), and these terms—RER and RQ—are sometimes used interchangeably (Walsberg & Wolf, 1995). High RQ values (near 1.0) are associated with carbohydrate oxidation; low values (near 0.7) are thought to reflect triacylglycerol oxidation, while values in between reflect a mix of fuels or protein oxidation, the latter often assumed to be negligible.

These values for carbohydrates and triacylglycerol thus provide fixed points for triangulating fuel mixture from measurements of exhaled breath (Péronnet & Massicotte, 1991).

Difficulties in applying this technique usually involve estimating the contribution of protein or interpreting values that lie outside of the "normal" range. It is not uncommon, for example, to observe values below 0.7, especially in birds (King, 1957; Mellen & Hill, 1955; Walsberg & Wolf, 1995). In these cases, deviation beyond the expected range has primarily been attributed to the nonrespiratory loss of CO_2, causing a mismatch between RER and RQ (Walsberg & Wolf, 1995), fatty acid desaturation (Owen et al., 1998), gluconeogenesis from amino acids (Schutz & Ravussin, 1980), or ketone excretion (Schutz & Ravussin, 1980). Rarely has the validity of the 0.7 value for fat oxidation been questioned, however. Here, we reexamine the basis for assigning 0.7 to the RQ for lipid oxidation and survey the literature on the varied natural fat compositions of animals. Based on this survey, we conclude that the RQ for lipid oxidation can reach at least as high as 0.73 in fasting wild animals.

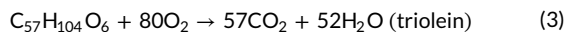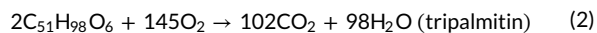## 1.1 | Historical perspectives on RQ for lipid oxidation

The expectation that oxidizing glucose will produce an RQ value equal to unity can be derived from stoichiometry (Equation 1).

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O \qquad (1)$$
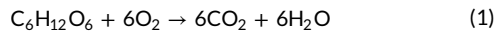
Six CO_2 molecules are produced while six O_2 molecules are consumed. Empirical measurements demonstrate that RER values close to 1.0 do indeed occur in cases of glucose oxidation (Groom et al., 2019), although occasionally higher values are also observed, perhaps due to lipid synthesis (King, 1957; Levin et al., 2017).

Protein has an expected RQ that varies between 0.696 and 1.021, depending on the nitrogenous waste produced (King, 1957). In practice, many investigators assume negligible protein oxidation or must measure nitrogenous waste excretion to calculate the non-amino acid RQ (Owen et al., 1998).

There is no single stoichiometric calculation that can be applied to triacylglycerol oxidation because the identity of the individual fatty acid moieties making up each triacylglycerol molecule will affect this stoichiometry. For example, stoichiometric calculation for the oxidation of tripalmitin (which has three palmitate moieties; C16:0) will yield an RQ of 102/145, or approximately 0.7034 (Equation 2). If the triacylglycerol instead has three oleate (C18:1ω9) moieties (triolein), the expected RQ is 57/80, or 0.7125 (Equation 3).

$$2C_{51}H_{98}O_6 + 145O_2 \rightarrow 102CO_2 + 98H_2O \text{ (tripalmitin)} \qquad (2)$$

$$C_{57}H_{104}O_6 + 80O_2 \rightarrow 57CO_2 + 52H_2O \text{ (triolein)} \qquad (3)$$

Early investigators took primarily stoichiometric approaches (often based on elemental analysis of adipose tissue) to estimate the expected RQ for fat oxidation and subsequently made broad claims about the universality of their results. In his influential text *The Elements of the Science of Nutrition*, Lusk calculated the expected RQ for tripalmitin as in Equation (2) (Lusk, 1917). But he also noted the complexity of naturally occurring animal fats and cited the elemental analysis of human fat[1] by Lehmann et al. (1893), which provided a stoichiometric estimate of 0.71. Another analysis of human fat provided a value of 0.713 (Zuntz & Loewy, 1909), which was also noted by Lusk. Importantly, Lusk claimed that RQ for lipid is nearly constant because most fat compositions were fairly similar, being composed primarily of palmitate, stearate (C18:0), and oleate (Lusk, 1917). To produce a table of RQ values and corresponding fuel mixtures, Lusk followed the table of Zuntz and Schumburg (1901), which was based on an RQ for lipids equaling 0.707, determined from the burning of "animal fat" ("thierisches Fett"; Zuntz, 1897), presumably obtained from a pig, dog, or other terrestrial mammal.

Krogh (1916) wrote that fat composition varies only a little, provided an elemental composition of "average" fat (RQ = 0.707), and partially reproduced the table of Zuntz and Schumburg (1901). Later Schmidt-Nielsen (1997), citing Lusk, would adopt 0.71 as the RQ for lipid in his animal physiology text. Brody (1964) noted that different fatty acids can produce different RQs and even noted that short-chain fats have RQs reaching 0.8. Nonetheless, he stated that the RQ for "mixed fat" is 0.71, again referencing Lusk, and reprinting Lusk's table of RQ and fuel mixture values (ultimately derived from Zuntz and Schumberg). In his now classic book *The Fire of Life*, Kleiber used the stoichiometry of tripalmitin and triolein oxidation to estimate RQ for lipids (Kleiber, 1961), and also provided an example of "average fat" that yielded an RQ of 0.708, thus perpetuating the idea of a universal average fat composition. Other investigators similarly have chosen to use the RQ for tripalmitin, or that of a mixed fatty acid composition with similar stoichiometry to that found in human triacylglycerols to assign an RQ value to 100% fat oxidation (Ferrannini, 1988; Frayn, 1983; Péronnet & Massicotte, 1991; Simonson & DeFronzo, 1990). Modern animal physiology textbooks generally present 0.70 or 0.71 as the theoretical RQ for lipid oxidation (Hill et al., 2016; Randall et al., 2002), but potential deviation from these values based on different fat compositions is not normally considered. Thus, the assumed RQ for lipid oxidation has historically been based on a very small selection of fat compositions from a handful of terrestrial mammals, primarily humans. Furthermore, this RQ for lipids has been assumed to vary little across species, despite no apparent assessment of fat composition beyond this limited set of terrestrial mammals.

2 | HOW DOES RQ VARY AMONG FATTY ACIDS?

Based on stoichiometric calculation, the RQs for the oxidation of the most common fatty acids are presented in Table 1. In general, RQ increases with an increasing number of double bonds and decreases with the length of the carbon chain (Figure 1). For complete oxidation of triacylglycerol, these RQ values range from 0.691 to 0.762. The common fatty acid stearate has a value below 0.7, while poly-unsaturated fatty acids range much higher, reaching 0.762 in docosahexaenoate (C22:6ω3). If only the fatty acid moiety is oxidized (but not the glycerol moiety, perhaps due to gluconeogenesis from glycerol), the RQ is slightly lower (Table 1), although we expect this would not normally occur under fasting conditions.

3 | HOW DOES RQ FOR FAT OXIDATION VARY ACROSS VERTEBRATE TAXA?

3.1 | Approach

Given the historical reliance on terrestrial mammals for calculating lipid RQ, we were curious as to how the RQ for lipid oxidation would vary across diverse vertebrate taxa rather than just the few mammals that
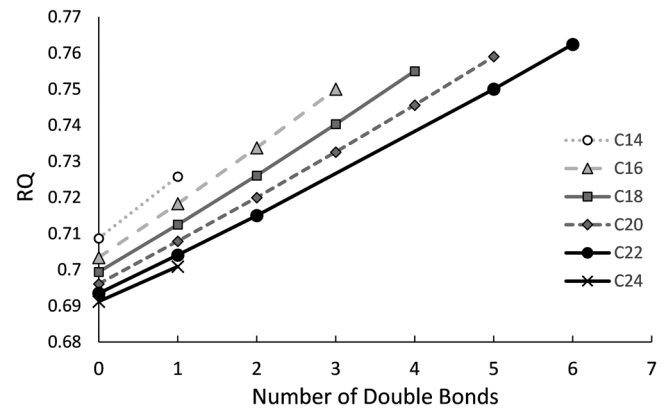
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[1]Lusk (1917, p. 59) claims this elemental analysis was obtained from lard, although the original work (Lehmann et al., 1893, p. 179) states that this calculation was based on the analysis of human fat ("*menschliche Fett*").

TABLE 1 Respiratory quotient (RQ) values associated with common fatty acids

Fatty acid name	Fatty acid formula	RQ (including glycerol moiety)	RQ (fatty acid only)
Myristate	14:0	0.7087	0.7
Myristoleate	14:1	0.7258	0.7179
Palmitate	16:0	0.7034	0.6957
Palmitoleate	16:1	0.7183	0.7111
Hexadecadienoate	16:2	0.7338	0.7273
Hexadecatrienoate	16:3	0.75	0.7442
Palmitodonate	16:4	0.7669	0.7619
Stearate	18:0	0.6994	0.6923
Oleate/Elaidate	18:1	0.7125	0.7058
Linoleate	18:2	0.7261	0.72
Linolenate	18:3	0.7403	0.7347
Steridonate	18:4	0.7550	0.75
Arachidate	20:0	0.6961	0.6897
Eicosenoate	20:1	0.7079	0.7018
Eicosadienoate	20:2	0.72	0.7143
Eicosatrienoate	20:3	0.7326	0.7272
Arachidonate	20:4	0.7456	0.7407
Eicosapentaenoate	20:5	0.7590	0.7547
Docosanoate	22:0	0.6935	0.6875
Erucate	22:1	0.7041	0.6984
Docosadienoate	22:2	0.7150	0.7097
Docosapentaenoate	22:5	0.75	0.7458
Docosahexaenoate	22:6	0.7624	0.7586
Lignocerate	24:0	0.6912	0.6857
Nervonate	24:1	0.7009	0.6957

FIGURE 1 Respiratory quotient (RQ) for lipid oxidation based on stoichiometry of oxidation of several common fatty acids (assuming complete oxidation of a triacylglycerol containing three copies of the fatty acid). Fatty acids of a given chain length, but varying in the number of double bonds, are joined by lines for ease of viewing. RQ decreases with increasing chain length, and increases with increasing number of double bonds
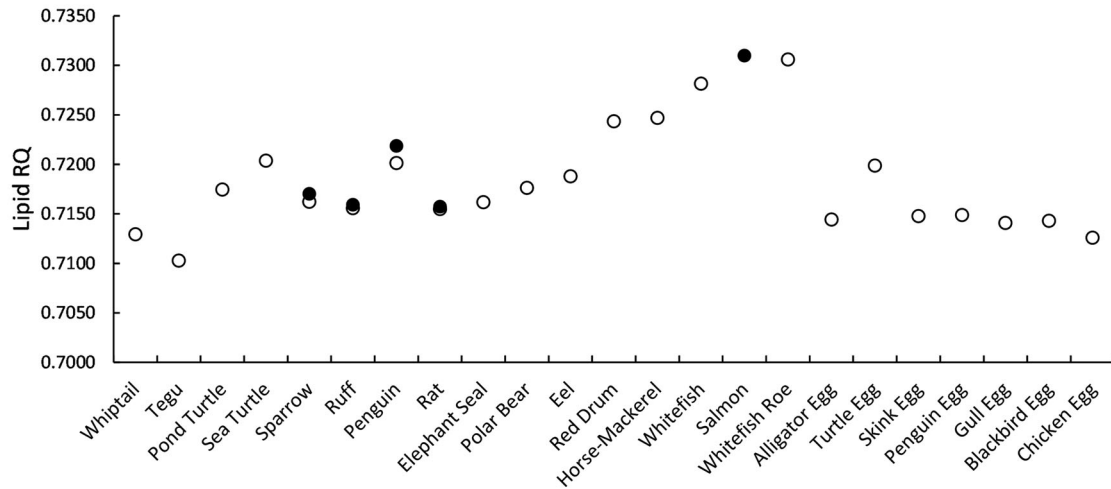
of major vertebrate groups while seeking to address the following questions.

First, we wanted to know whether aquatic and marine species would have higher lipid RQs than terrestrial species. Long-chain poly-unsaturated fatty acids like docosahexaenoic acid are more abundant in aquatic ecosystems than terrestrial ones (Gladyshev et al., 2013; Hixson et al., 2015), and yield high RQs upon oxidation (Table 1). Therefore, we predicted that aquatic/marine animals would have high RQs for fat oxidation, as would animals that feed in aquatic habitats and, therefore, might store large amounts of docosahexaenoic acid. In addition, we were interested in knowing whether any such pattern extends to eggs as well. Egg yolk fatty acids might reflect maternal fuel lipids, or alternatively, could vary little among taxa, perhaps constrained by common developmental requirements for specific fatty acids.

Second, we were curious if selective mobilization of fatty acids from adipose tissue could affect the RQ for fat. Hydrolysis of fatty acids is a nonrandom process, such that fatty acids are not mobilized in a fashion exactly proportional to the makeup of adipose tissue (Price & Valencak, 2012; Raclot, 2003). Oxidation of fatty acids by muscles is also selective (Hagenfeldt & Wahren, 1968; Price et al., 2011, 2014; Sidell et al., 1995). Therefore, the RQ for lipid metabolism based on stored triacylglycerol composition might differ from that of the lipids actually oxidized. In particular, fatty acids that are unsaturated and shorter chained are associated with higher RQs (Figure 1) and are also selectively mobilized (Raclot, 2003); therefore, we predicted selective mobilization would result in an upward shift in RQ.

3.2 | Results

For the mammals and most reptiles and birds, lipid RQ did not vary greatly and was around 0.715 (Figure 2). This coincides largely with historical assumptions regarding fat, and these species had fat stores

have been studied. We took the approach of surveying published literature on fatty acid compositions of fuel lipids (adipose tissue, intramuscular triacylglycerols, or plasma free fatty acids) from various species. For a given fatty acid composition, we multiplied the molar percent of each fatty acid by the number of carbon, hydrogen, and oxygen atoms comprising each fatty acid (assuming it was esterified to glycerol), summed these across all fatty acids in the entire composition, and then balanced the resulting oxidation equation. The RQ for fat oxidation depends on the composition of both dietary inputs and stored fatty acids. Our approach ignores the dietary aspect and only focuses on the RQ that would be obtained if an animal oxidized fat mobilized from its adipose tissue, as would be the case in a fasting animal. Fasting is often the state in which RQ is measured, and our analysis can also be applied to dietary components if their fatty acid composition is known.

We did not catalog all fatty acid compositions published for vertebrates; instead, our goal was to obtain representative samples

FIGURE 2 RQ for lipid oxidation based on fatty acid composition (assuming complete oxidation of triacylglycerol) for several species of vertebrates. Open circles denote RQ based on fatty acid composition of total lipids in adipose tissue (whiptail lizard, tegu lizard, slider turtle, loggerhead sea turtle, elephant seal, and polar bear), neutral lipids in adipose tissue (white-crowned sparrow, ruff, emperor penguin, and rat), neutral lipids in muscle (American eel, horse-mackerel, red drum, and whitefish), or whole yolk (whitefish roe, alligator, river turtle, skink, penguin, gull, red-winged blackbird, and chicken). Filled circles denote RQ based on nonesterified fatty acids mobilized from adipose tissue (rat, white-crowned sparrow, ruff, and penguin), or present in plasma (fasting sockeye salmon). RQs were based on data from (Ackman et al., 1971; Ballantyne et al., 1996; Bandarra et al., 2001; Best et al., 2003; Brian et al., 1972; Chan, 1995; Ferreira et al., 2009; Grahl-Nielsen et al., 2003; Groscolas, 1990; Guitart et al., 1999; Kaitaranta, 1980; Otwell & Rickards, 1981; Price et al., 2008, 2018; Raclot & Groscolas, 1993; Speake & Thompson, 1999; Speake et al., 1996, 2003). For salmon we used data from males from Site 1 (Ballantyne et al., 1996); for drum we used data from animals fed the menhaden oil diet (Chan, 1995); and generally we used data from wild-caught adults when multiple ages or origins were available

that consisted primarily of palmitate, oleate, and stearate. However, the greater quantity of polyunsaturated fatty acids in fish, particularly docosahexaenoate, resulted in higher lipid RQ values in the penguin and the fish species, reaching over 0.73 in salmon. Differences among taxa were also present in eggs: whitefish roe had a lipid RQ over 0.73, while most bird and reptile eggs had lipid RQs under 0.715 (Figure 2). Interestingly, some animals from "terrestrial taxa" but having "aquatic diets" (polar bear, elephant seal, and ruff) did not have particularly high RQs. These animals might have adipose fatty acid compositions that are determined in taxon-specific ways, or alternatively, their fatty acid compositions may be heavily influenced by de novo lipid synthesis more so than by dietary fat composition.

We found a deviation between the RQ based on adipose tissue and the RQ based on the composition of fatty acids found to be mobilized in several selective mobilization studies (Figure 2); however, this deviation was slight (maximum difference of 0.0017).

4 | DISCUSSION

The range of RQ values produced by oxidation of commonly stored fatty acids is much wider than normally considered. Although a few values fall below 0.7 including that of stearate, they are only barely so, and cannot account for the substantially depressed values of RQ occasionally observed in birds and other species. On the other hand, quite

a few fatty acids have RQs that are substantially greater than 0.71, and this can have important effects on the average lipid RQ. Based on the normally assumed range of RQ and average human fatty acid composition, an observed value of 0.73 would likely lead an investigator to conclude that mostly fat is being oxidized, but that there is some amount of protein or carbohydrate oxidation (if protein oxidation is assumed to be nil, an RQ of 0.73 would suggest approximately 10% carbohydrate oxidation (Péronnet & Massicotte, 1991). Our analysis indicates that this assumption would be reasonably accurate for most terrestrial vertebrates like mammals and birds, but would be incorrect for some species, particularly fish, many of which should achieve RQs exceeding 0.73 while oxidizing only lipid. As another example of how results may be affected, a recent study using an RQ for lipid of 0.71 concluded that fasting zebrafish oxidized carbohydrates as 42% of their fuel mixture (Ferreira et al., 2019). Assuming an RQ for lipid of 0.73, we calculate carbohydrates at only 39.5% of the fuel mixture (about 6% lower). Therefore, we urge investigators to use known fatty acid compositions or take into account the taxon and habitat when making an assumption regarding the RQ for lipids, particularly when studying aquatic or marine species. As a practical matter, we suggest assigning 0.725 as the lipid RQ for cold-water fish when the fatty acid composition of fuel lipid is unknown.

Our analysis indicated little effect of the selective mobilization of fatty acids from adipocytes on lipid RQ. We did not consider the effects of selective catabolism, which could potentially be additive

with those of selective mobilization. Nonetheless, the present analysis suggests that researchers need not take into account the effects of selective mobilization for determining fuel mixture from RQ measurements unless a particularly high degree of accuracy is required.

ACKNOWLEDGMENT

CONFLICT OF INTERESTS

The authors declare that there are no conflicts of interests.

DATA AVAILABILITY STATEMENT

The data used to create Figure 2 were compiled from various sources (see Figure legend), and are provided in Supplementary File.

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