Rapid mobilization of abdominal fat in migrating eared grebes

Lorian Cobra Straker and Joseph R. Jehl Jr

Eared grebes *Podiceps nigricollis*, like shorebirds and other long-distance migrants, lay down large amounts of fat to power their journeys. To investigate the pattern of how fat and soft tissue might be mobilized, we used grebes killed in migration and applied computed tomography to reconstruct how stores in the chest, thorax, and abdomen were reduced as body weight decreased. Fat and soft tissue were each mobilized at a constant rate through the entire migration. Fat stores in birds embarking on migration were greater in the abdomen than thorax than chest. In contrast to previous studies indicating that abdominal fat was mobilized first, we found that fat from all areas was mobilized concurrently, but that abdominal fat was catabolized at a greater rate. We suggest why this pattern might be advantageous, consider whether inter-depot differences in fat composition might be involved, and note possible energetic consequences. Whether our findings pertain to other obese or long distance migrants remains to be determined.

The biology of avian fat has been the subject of intense current interest and there is now an extensive literature on its biochemistry, composition, mobilization, and role in nutrition, migration and energetics (Blem 1976, 1990, Ramenofsky 1990, McWilliams et al. 2002, 2004, Pierce et al. 2005, Price et al. 2008, Guglielmo 2010, Price 2010, Pierce and McWilliams 2014). It has long been known that birds preparing for long-distance migration (e.g. shorebirds) or prolonged fasting (e.g. incubating penguins) lay down huge fat deposits to meet anticipated energy demands. Shorebirds, for example, can double their weight before setting off, such that fat content (fat/body weight) can reach 45% or more (Jehl 1997a). The apparent maximum is 54.9%, as reported in juvenile bar-tailed godwits *Limosa lapponica* embarking on a nonstop flight from Alaska to New Zealand (Piersma and Gill 1998). Wilson’s phalaropes *Phalaropus tricolor* at a similar level of obesity become too heavy to take off (Jehl 1997a).

Fat is stored in discrete areas called depots. King and Farner (1965) recognized 13, but the distinctions proved impracticable for most studies (Battley and Piersma 1997) and others have tended to combine them by 3–4 general areas of the body. Indeed, grouping is inevitable in long distance migrants, which store fat in every conceivable space, filling the body cavities, infiltrating muscles and viscera, and wrapping the body in a near-continuous sheet.

McCabe (1943) provided the first detailed overview on the sequence of fat deposition. The general pattern is for sites to begin filling in the following order: furcula, axilla, and abdomen (De Sante et al. 2008). Blem (1976) reported that subcutaneous fat was deposited first. In the red knot *Calidris canutus* subcutaneous fat is deposited at a steady rate, whereas in that species and the great crested grebe *Podiceps cristatus* abdominal and intestinal fat are more heavily deposited after other areas are filled (Piersma 1984, Battley and Piersma 1997). Wirestam et al. (2008) greatly expanded our knowledge by using Magnetic Resonance Imaging (MRI) to make repeated observations of the spatial allocation of stores through the fattening process in several passerines. In contrast to detailed information at the cellular level regarding ‘the physiological and biochemical mechanisms birds use to fly while burning fatty acids’ (Guglielmo 2010) it is the paucity of information regarding the broad pattern of fat mobilization from specific areas of the body. In incubating Canada geese *Branta canadensis* it involves the simultaneous catabolism of abdominal and subcutaneous fat, with subcutaneous deposits depleted last (Raveling 1979). In the same species Austin (1993) determined relatively rapid mobilization from the thigh. Piersma (1984) and Blem (1990) reported that intraperitoneal fat is the first to be mobilized during starvation or stress. Blem (1976) noted that early deposition and late use of subcutaneous fat may be linked to possible benefits of insulation, but acknowledged the phylogenetic limitations of the data and cautioned that patterns and variations may be affected by daily or seasonal requirements of different species.

Our major interest concerns the pattern by which fat stores are mobilized in birds carrying high loads during an extended migration. Is it depleted concurrently from all areas of the body, or are some depots used first? And how, for example, might the pattern of deposition and depletion affect the aerodynamics of such birds (Hedenström 1992,
To approach these questions we used carcasses of eared grebes *Podiceps nigricollis* killed in migration, and applied computed tomography (CT) to measure the amount and distribution of fat over the weight range expected in that species’ uninterrupted migrations (Jehl 1997b). Although grebes avoid flying during the day and consequently do not make long non-stop flights, their fat content on setting off (≈ 40%) rivals or exceeds that of shorebirds that fly far greater distances without stopping. The sometimes puzzling extreme weight changes in eared grebes over the annual cycle have been discussed previously (Jehl 1997b). Here we report details of their differential allocation and mobilization of fat stores and inquire whether the results may apply to the energetics of more extreme migrants.

**Study species**

The eared grebe is a common breeder throughout the interior western United States and Canada. After nesting, the majority of the population moves quickly to Great Salt Lake, Utah, and Mono Lake, California, to molt and stage for up to several months and feed on the abundant invertebrates. During this post-breeding migration, which in some cases takes only 2–3 nights, the total distance covered may be as much as 1500 km (Jehl and Henry 2010). During the staging period adult grebes can fatten to > 600 g; this weight combined with atrophy of the breast muscles renders them flightless. When food runs out they catabolize excess fat, reorganize body composition, and depart at a continuous flight was 10–14 h.

The weight ranges of birds in any sample were too small to encompass that expected of grebes in normal migration. Combining samples allowed us to create a series of 21 AHY (adult) grebes, whose weights (238–469 g) were spread at 10–30 g intervals over the range observed in migrants moving to and from GSL (Jehl 1997b). This allowed us to examine changes in fat and body composition during migration in an ‘average’ migrant. To minimize variation we excluded juveniles (autumn) and first-year birds (spring), which are on a different weight trajectory (Jehl 1988, 1997b, Ellis et al. 2016), except for our lightest bird in spring, which was a first year. Previous studies (Jehl 1997b, Jehl and Henry 2010) have established that most adults, in spring or fall, usually depart at weights of 400–450 g. We assumed that the pattern of fat mobilization would be similar, if not the same, in either season, with differences in fat content being dependent on the size of the bird or how successful an individual may have been in obtaining resources prior to departure. We acknowledge that birds in different flights might start off with slightly different body composition depending on their timing and place of origin; data to test this are unavailable.

To confirm that weight differences between individuals derived largely from fat content, we weighed skeletons of museum specimens (n = 18, mean = 13.9 ± 1.56 g), which showed that skeletal weight has little effect. Although soft tissue is catabolized in migration (see below), the mean difference between our samples was small (maximum of 12 g: CC = 134.5 ± 11.03 g; DPG = 128.0 ± 13.24 g; GR = 122.5 ± 7.34 g). Accordingly, we combined specimens from all samples to understand the fat mobilization pattern of a typical migrant.

All specimens were frozen after salvage and thawed for CT imaging. Scanning was done at the Dept of Anthropology, Smithsonian Inst., on a SOMATOM Emotion 6 CT-scanner at a voltage of 110 kV, tube current 80 mA, and slice thickness of 0.63 mm. Rendering of 3D volume images of whole birds was done in the open source medical image viewer software Horos (ver. 1.0.7, <www.horosproject.org>). We used Mimics software package

**Methods**

Historically measurements of body composition and fat content have involved invasive and destructive techniques. Recently, non-invasive methods have become available (e.g. total body conductivity, D₂O dilution, fat score; McWilliams and Whitman 2013). In addition, imaging technology such as MRI and magnetic resonance spectroscopy (MRS) have been shown to provide highly informative measurements and thus allow us to consider changes in different body regions (Berthold et al. 2001, Wirestam et al. 2008, Hedenström et al. 2009). As in MRI and MRS, CT imaging has shown similar potential for measuring fat distribution and volume in living animals (Judex et al. 2010). As noted above, the annual migration of the eared grebe in North America occurs in three main phases. We used CT to examine carcasses of birds that died in three separate events to study the sequence of fat mobilization.

**Post-breeding migration**

Salvaged over several seasons (2001–2005) from waste water ponds near Green River, Wyoming (GR), this sample comprised birds near the finish of a direct 2–3 d flight from breeding areas to Great Salt Lake. The majority likely originated in the Prairie Potholes Region of North Dakota. We estimate their time in actual flight at 16–20 h (Jehl and Henry 2010).

**Post-staging migration**

Specimens from Cedar City, Utah (CC) originated at Great Salt Lake (GSL) and were downed by snowstorm 4.5–6 h after setting off on the night of 11–12 December 2011 (Jehl et al. 2012).

**Spring migration**

Specimens from Dugway Proving Ground, Utah (DPG) were part of a major flight that encountered bad weather on 15 April 2013 (Ellis et al. 2016). These birds almost surely had a common origin, either at the Gulf of California, Mexico, or the Salton Sea, California; their estimated time in continuous flight was 10–14 h.

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(Materialise NV, Leuven, Belgium) to establish gray scale thresholds to automatically differentiate body components (bone, soft tissue, fat). From this we created an integrated series of images along the length of the body (segmentation) and calculated the volume of specific tissues in a designated area. Even with this technology, however, it was not possible to create threshold scales that could fully distinguish muscle and other organs (similar density) or account for the small amount of fat suffused in liver or muscles (Ross et al. 1991) (up to 20.97% dry wt in the grebe pectoralis; Jehl et al. 2015). This technical issue is related to X-ray imaging of soft tissues in which tissue differentiation and reconstruction precision is dependent on equipment’s settings and sensitivity. Structure spatial complexity of tissues (e.g. protrusions, small surface irregularities and infusion) is best resolved by the software when neighboring tissues are assigned much different attenuation coefficients (Hu) (Hillebrand et al. 2010). Thus, values of fat content presented here are conservative but reliable, whereas those of soft tissue are inflated by undetectable amounts of fat.

To determine fat volume we divided the carcass into three sections that hold virtually all of the fat stores: 1) chest (C): base of the neck to the rostrum of the sternum. 2) Thorax (T): body along the entire length of the sternum. 3) Abdomen (A): posterior tip of the sternum to the vent; this include the femur and upper tibiotarsus.

Not included were head, mid and upper neck, wings and lower leg, as these parts do not hold enough fat to affect migration energetics. To convert volume to weight we collected equal volumes of fat and pectoral muscle, determined their relative weights (to 0.001 g) and used the results (fat: 0.958 g (2.5 ml) of fat and pectoral muscle, determined their relative weights in the whole bird and in each body region. Tissue weights (total fat or fat depots or soft tissue) were subtracted from body weights to ensure that tissue weights were not having any influence on Ancova results or on the regression line slopes.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.dd00m> (Straker and Jehl 2016).

### Results

Variables for carcasses in this study are presented in Table 1. CT-scan reconstructions of the extreme grebes are presented in Fig. 1. Regression lines for fat content using total fat extraction and CT were not significantly different (Ancova: F = 0.06; p = 0.816) (Fig. 2). On the other hand, there were important differences in total fat, with CT detecting 67–73% of total extraction throughout all specimens. We attribute the discrepancies mainly to challenges in measuring infused fat in soft tissues (e.g. flight muscle and liver) and, to a lesser degree, to the fat in the areas we did not consider. Nevertheless, the consistency of CT in comparison to other techniques – here and in other studies (Ross et al. 1991, Hillebrand et al. 2010) – justifies its use in analysing patterns and rates of intra-site catabolism over a range of body size, and supports our procedure of using specimens from different phases of migration to create an ‘average’ migrant.

Fat volume within each body section varied with the bird’s state of migration. In our lightest bird (238 g) it was relatively evenly distributed (CT:A ratio 1:1:1.3); in the heaviest it was concentrated in the abdomen (CT:A ratio 1:1.4:2.9). Figure 3 presents fat and soft tissue profiles of a migrating grebe whose weight decreased in flight

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<table>
<thead>
<tr>
<th>ID</th>
<th>Age/sex</th>
<th>Body weight</th>
<th>Season</th>
<th>Hours in flight</th>
<th>Computed tomography</th>
<th>Chest fat (g)</th>
<th>Thorax fat (g)</th>
<th>Abdomen fat (g)</th>
<th>Soft tissue (g)</th>
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from 469 to 238 g. Both tissues were catabolized concurrently, apparently at a constant rate. However, when apportioned by body region (Fig. 4), we found that abdomen fat was catabolized $2 \times$ faster than that of the thorax, and nearly $4 \times$ that of the chest (Ancova: $R^2 = 0.928$; $F_{(6, 57)} = 122.5; p < 2.2\times10^{-16}$). Consequently, stores were depleted earlier in the abdomen (intercept 240 g) than in the thorax (219 g) and chest (200 g). Figure 5 illustrates change in fat distribution in three body regions as body weight declines in migrants.
Heitmeyer and Fredrickson (1990) also noted the greater lability of abdomen fat in mallard *Anas platyrhynchos*. Several factors might influence these storage and mobilization patterns. The prominence of abdominal fat is well known (Hedenström et al. 2009) and easily understood because the abdominal cavity is expansible and thus provides by far the greatest potential storage space. It is also nearest the liver and thus can be more rapidly accessed. Its prominence is further magnified in the eared grebe and other species that shrink their digestive organs before migrating, thereby making room for even more fuel (Jehl 1997b, Piersma and Gill 1998, Gill et al. 2005). Greater vascularization of the abdomen catabolized fastest. Heitmeyer and Fredrickson (1990) also noted the greater lability of abdomen fat in mallard *Anas platyrhynchos*.

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**Discussion**

When fatty acids are released into the circulation, they ‘bind quickly to albumin... [and then] may be transported either to target tissues directly for uptake and utilization or routed to the liver... for ultimate release into the circulation and target tissues’ (Ramenofsky 1990: 219). Our goal was to determine whether there was any sequence in which various deposits were mobilized in migrants with large fat loads. Using the eared grebe as a model we found that a) fat stores in birds at the start of migration were greater in the abdomen than thorax than chest; b) fat was mobilized concurrently in all regions; but c) stores in the abdomen were catabolized fastest. Heitmeyer and Fredrickson (1990) also noted the greater lability of abdomen fat in mallard *Anas platyrhynchos*.

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abdominal region could also affect rapid uptake. Piersma (1984: 124) suggested that ‘early mobilization... of abdominal fat is a general phenomenon’, but in grebes all regions were accessed concurrently. This suggests that the purported early mobilization of abdominal fat may be an illusion stemming from its higher rate of catabolism.

Considering regional differences in isolation, however, may be an oversimplification. Fatty acid composition can vary among depots (Austin 1993, Crespo and Esteve-Garcia 2001, Pierce et al. 2005, Price et al. 2008) and this may account for some differences in inter-depot mobilization rates. And if some depots are mobilized selectively during migration (McWilliams et al. 2004, Pierce and McWilliams 2014), this would hint at an optimal way to distribute fatty acids to maximize flight performance. For instance, we might expect abdominal depots to have a high concentration of unsaturated and short-chain fatty acids, because they are mobilized more readily than saturated fatty acids (Blem 1976, Price 2010). While preferential mobilization has yet to be demonstrated in migrants (Pierce et al. 2005), the possibility should not be dismissed inasmuch as it has been reported in fasting emperor penguins Aptenodytes forsteri (Groscolas 1990) and, recently, in two very different mammals (Arriola et al. 2013, Price et al. 2013).

Mechanical considerations are also relevant. Obesity results in increased wing-loading and requires increased wing beat frequency (Klassen 1996, Videler 2005), and the fat loads needed for long migrations impose parasitic power costs due to increased frontal area and drag (Kvist et al. 2001, Pennycuick 2008, Wirestam et al. 2008). This raises the question of how best to distribute fuel. At the start of migration a 469 g grebe holds nearly three times as much fat in the abdomen than chest, and this inequality will affect its center of gravity, flight balance, and positioning of different body parts (Videler 2005). Hedenström et al. (2009) suggested that the concentration of fat in the anterior and posterior areas, rather than uniformly along the body, may be an adaptation to minimize drag. It seems to us, however, that rather than being a solution to an aerodynamic challenge, allocating large amounts of fat in the abdomen is the only way to store sufficient fat to support very long flights, and that its rapid mobilization may be a way to redress the aerodynamic problems it causes.

Soft tissue (muscle) is also catabolized in migration, and may contribute 5–15% to total energy demand (McWilliams et al. 2004). Figure 3 indicates that our ‘average’ migrant would catabolize 16.4 g (11.3% of take-off) as its body weight dropped from 433 (295 g fatBW) to 280 g (158 g fatBW). This is similar to the = 22 g loss from major body components as calculated by comparing a 433 bird departing Mono Lake (Jehl 1997b, Table 1, sample 5) with those of a 280 g bird arriving at Green River (Jehl and Henry 2010, Table 3). However, our data are not definitive; our estimate of soft tissue catabolized in the ‘average’ migrant is affected by the gray scale problem noted above, and by the need for additional weights for some body components of actual migrants at the time of departure. Other studies will be needed to test whether the patterns of fat and soft tissue mobilization in grebes apply to long distance migrants as well.

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