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SHORT COMMUNICATION

High carbohydrate consumption increases lipid storage and promotes migratory flight in locusts

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ABSTRACT

Migration allows animals to track favorable environments and avoid harmful conditions. However, migration is energetically costly, so migrating animals must prepare themselves by increasing their energy stores. Despite the importance of locust migratory swarms, we still understand little about the physiology of locust migration. During long-distance flight, locusts rely on lipid oxidation, despite the fact that lipids are relatively rare in their leaf-based diets. Therefore, locusts and other insect herbivores synthesize and store lipid from ingested carbohydrates, which are also important for initial flight. These data suggest that diets high in carbohydrate should increase lipid stores and the capacity for migratory flight in locusts. As predicted, locust lipid stores and flight performance increased with an increase in the relative carbohydrate content in their food. However, locust flight termination was not associated with complete lipid depletion. We propose potential testable mechanisms that might explain how macronutrient consumption can affect flight endurance.

KEY WORDS: Energy stores, Flight endurance, Locusts, Macronutrients, Migration, Nutrition

INTRODUCTION

Many animals migrate from one type of habitat to another across space and time (Aidley, 1981; Fudickar et al., 2021), allowing them to maximize fitness, survival, and growth in fluctuating environments (Brönmark et al., 2008; Dingle and Alistair Drake, 2007; Seebacher and Post, 2015). Migration is usually energetically costly and so requires a variety of adaptations to promote vagility and energetic efficiency (Malik et al., 2021; Milner-Gulland et al., 2011). Migratory birds, which are the most studied among migratory animals, have evolved navigational (Able, 1980), morphological (Vágási et al., 2016) and physiological (Biebach, 1990; Laguë, 2017) mechanisms that enable them to fly hundreds to thousands of kilometers. Despite the unique adaptations of any migrating animal, one of the most important factors for successful migration is building up energy stores to fuel locomotion. While there is some understanding of the nutritional requirements of migrating vertebrates (Kenney et al., 2020; Metcalfe and Furness, 1984; Parrish, 2000), dietary requirements for migrating insects remain less studied.

Migration is fueled primarily by carbohydrates and lipids, which must be acquired by animals before and during migration (Dingle, 2006). Proteins are important as building blocks but are rarely used as migratory fuels because oxidation of proteins and amino acids produces nitrogen waste that is energetically costly to remove, potentially involves loss of water and can be toxic if not excreted (Wright, 1995). Birds and other animals ingest fruit and seeds that are rich in sugars and lipids, respectively (Jenni and Jenni-Eiermann, 1998). Carbohydrates can be stored to a limited extent as glycogen, but the capacity to store energy-dense lipids is much higher in most migratory animals (Bairlein, 2002). Thus, animals preparing for migration typically ingest high fat diets or convert ingested carbohydrates to lipids. For example, the yellow-rumped warbler (*Setophaga coronate*) consumes a high carbohydrate diet to accumulate fat and improve migratory flight (Guglielmo et al., 2017). Many migratory insectivorous birds go through a seasonal diet shift where they switch from foraging for insects (high protein food) during the summer, to fruits (high in sugars and fats) during the fall, before their migration (Domer et al., 2019; Klasing, 1998; McWilliams et al., 2004; Thompson and Willson, 1979). Some animals, such as the European eel (*Anguilla Anguilla*), do not eat during their entire migration; thus, they must store enough energy, usually as fat, for the entire journey (Van Ginneken et al., 2005). Some migratory birds can even double their mass before the migration starts (Klaassen, 1996). However, in some animals, especially insects, extra muscular lipids are not readily available at the beginning of flight and take some time to mobilize (Weber, 1988). For example, the kissing bug (*Panstrongylus megistus*) uses carbohydrates during the initiation of flight, then switches to lipids to fuel the rest of the flight (Canavoso et al., 2003).

Locust migrations are part of a complex ecological, economic and social system that can have dramatic effects on human livelihoods (Cease et al., 2015). They frequently undergo long-range migration, in some cases even crossing the Atlantic Ocean (Rosenberg and Burt, 1999). Locust flight physiology has been extensively studied over the past 70 years, yet their dietary requirements for flight are largely unknown. Pioneering studies of Weis-Fogh (Krogh and Weis-Fogh, 1951; Weis-Fogh, 1952), showed that for desert locusts (*Schistocerca gregaria*), flight duration depends on body lipid content. Later, researchers discovered that, besides the initial (15–30 min) flight, which is fueled by carbohydrates, longer sustained flights are fueled mostly by lipids (Beenakkers et al., 1981). Locusts and other herbivorous insects that have limited access to dietary lipids rely on dietary carbohydrates for short flights (Jutsum and Goldsworthy, 1976) and on *de novo* lipid synthesis – which fuels flight muscles, for longer flights (Gokuldas et al., 1988; Talal et al., 2020, 2021). Thus, long distance migratory capacity must heavily rely on fulfilling nutritional and fuel demands. Despite the importance of the link between migratory flight capacity and locust nutrition, only one study has been published testing how availability of dietary macronutrients affects flight performance. In that study, Mongolian locusts (*Oedaleus asiaticus*) reared on their preferred diet containing twice as much carbohydrate as protein (14% protein and 28% carbohydrate, by mass) showed increased

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migratory morphology and flew for longer times (flight was allowed to persist up to 120 min) (Cease et al., 2017). Here, we studied the effect of macronutrient balance on whole-day migratory flight performance using the migratory locust *Locusta migratoria*, which is one of the two most destructive locust species (Cullen et al., 2017; Pener and Simpson, 2009). We predicted that locusts reared on low protein, high carbohydrate diets will increase their body lipid stores and exhibit better flight performance compared with locusts reared on high protein, low carbohydrate diets.

MATERIALS AND METHODS

Animals

We tested flight in adult male migratory locusts *Locusta migratoria* (Linnaeus 1758). To establish our colony at Arizona State University (ASU), egg pods were brought in December 2019 (under USDA permit # P526P-19-03892) from the University of Haifa-Oranim, Israel; locusts for the colony were originally collected in 2014 from Hainan province, China. Locusts were reared in group cages (45.7×45.7×45.7 cm) on wheat grass, romaine lettuce and wheat bran *ad libitum*. Lab rearing conditions were 30.0±0.5% relative humidity, 14 h days at 34±0.5°C, 10 h nights at 25.0±0.5°C and supplementary heat was supplied during the day by incandescent 60 W light bulbs.

Artificial diets

Three artificial diets were made in our Arizona State University lab that varied in protein (p) and carbohydrate (c): 14p:28c, 21p:21c and 35p:7c (% protein and carbohydrate by dry mass). Diets were modified from those outlined by Dadd (1961) and modified by Simpson and Abisgold (1985). Proteins were provided as a mix of casein, peptone and albumen (3:1:1 ratio, respectively). Carbohydrates were provided using a mix of sucrose and dextrin (1:1 ratio). The rest of the ingredients in these diets included cellulose powder (58% of total weight of the dry artificial diets), salts and vitamins.

Experimental design

To test how dietary protein to carbohydrate (p:c) ratio affects locust flight performance, we collected ∼300 (equal sex ratio) newly molted 5th (final) instar nymphs and divided them equally into three diet treatments varying in p:c ratio (14p:28c, 21p:21c, 35p:7c). Each diet group was reared in a separate crowded cage (45.7×25.4×45.7 cm) and provided with their assigned artificial diet and six 50 ml water tubes sealed with cotton balls *ad libitum*. We continued to rear all locusts on their test diets until the flight performance experiment, which started when the locusts were 1-week-old adults.

We designed and built 15 tethered flight tunnels using PVC tubes (66.7 cm long×15.2 cm inner diameter) which were attached to electric fans (Vivosun Inline Duct Fan 6 in). To reduce air turbulence, all air flowed through ∼65 plastic tubes (1.5 cm diameter×9.5 cm long) at the inlet of each flight tunnel. Each flight tunnel produced an air flow speed of 11.1±1 km h^{-1}. To tether locusts, we attached a 3 mm magnet disk (using hot glue) to their pronotum; the magnet held locusts to ∼8-cm-long bolts that were secured ∼6 cm below the ceiling of the flight tunnel (Fig. 1).

We flew each (7–15 days old) adult male locust only once, up to 12 h. Each experiment started at 08:00 h and ended at 20:00 h, after which locusts were frozen and stored in −20°C for further lipid analysis. To record and analyze the flight performance, we used three Digital HD Video Camera Recorder (HDV-604S); each camera recorded five locusts.

Total body lipid extraction

To determine pre-flight and post flight body lipid content and lipid use during flight, we used post flight locusts as well as control locusts from each of the diet treatments. To decrease variation and control for locust age, we collected locusts from each diet treatment each day. Locusts were randomly assigned to the control or flight group. Because the locusts flying on the tethers for up to 12 h did not have access to food or water, we also did not provide the control locusts with food or water for 12 h. At the end of the day, locusts from both groups were frozen at −20°C.

We used chloroform extraction to measure body lipid content and calculate the change in body lipid mass for each diet treatment. Each locust was dried to a constant mass (∼48 h at 60°C) and then submerged in glass vials of chloroform, which were replaced daily for 3 days, after which locusts were dried and re-weighed (Loveridge, 1973).

Video analysis and statistics

We viewed and analyzed each video directly. Three variables were recorded: total flight time, longest single flight and number of stops. We defined a single flight as a flight that lasted ≥1 min and had no stops that lasted longer than 5 s. If the locust stopped for more than 5 s, it was considered a new flight when they started again. Total flight was the sum of all flight times. The longest single flight was the longest time a given locust flew without stopping for more than 5 s. Number of stops was calculated by counting the number of times the locust stopped for more than 5 s.

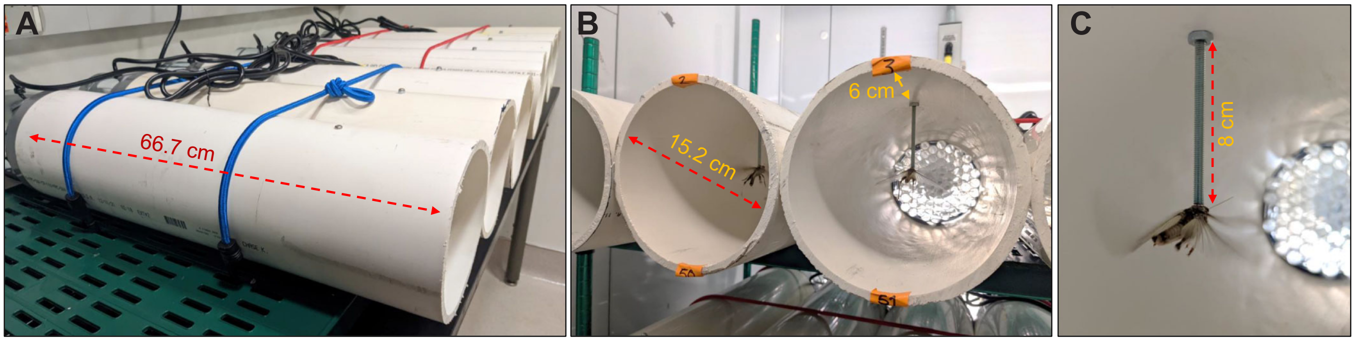

Fig. 1. Locust flight mill system. Each flight mill included a 66.7 cm PVC pipe (A) with a radius of 15.2 cm (B) with a booster fan connected to the end. To reduce turbulence, we inserted ∼65 small plastic pipes next to the fan (B,C). To attach a locust, we first glued a 3 mm magnet to its pronotum and attached it to an 8 cm bolt (C), positioned 6 cm inside the flight mill (B).

Statistical analyses were performed using the SPSS20 statistical software (IBM, Armonk, NY, USA). Prior to using parametric tests, the normal data distribution was confirmed using Shapiro–Wilk normality tests. For all flight performance parameters that were non-normally distributed (total and longest flight durations and number of stops), we used Kruskal–Wallis tests followed by Dunn's *post hoc* tests. We compared dry lean body mass (the remaining dry mass following lipid extraction) and absolute body lipid mass using two-way ANOVAs, followed by Bonferroni *post hoc* tests. To compare corrected body lipid content of locusts on different diet treatments and the effect of flight versus control, we used a two-way ANCOVA (with dry lean mass as a covariate), followed by Bonferroni *post hoc* tests. The raw data are available in supplementary material Tables S1–S3.

RESULTS AND DISCUSSION

Overall, locust flight performance increased with an increase of carbohydrate proportion in the diet. As the proportion of dietary carbohydrate increased, total flight time and the longest single flight duration both increased (Kruskal–Wallis: χ^2_2=20.014 and χ^2_2=18.206, respectively; P<0.001) (Fig. 2A), whereas the number of stops decreased (Kruskal–Wallis: χ^2_2=18.114, P<0.001) (Fig. 2B). Locusts that were reared on the carbohydrate-biased diet flew for twice as long and had half the number of stops compared with locusts that were reared on protein-biased diets (Fig. 2). Six out of 34 locusts fed the 14p:28c diet flew continuously for 12 h, whereas only one locust out of 35 from the 21p:21c diet treatment flew for 12 h, and no locusts from the 35p:7c diet group flew non-stop for the 12 h flight test.

Diet had a strong effect on body composition. Dry lean mass of carbohydrate-biased fed locusts was ∼8% lower than with the other diet treatments ($F_{2,107}$=7.531; P=0.001, Fig. 3A). In addition, dry lean mass decreased by ∼3.7% during flight in each of the diet treatments ($F_{1,107}$=4.353; P=0.036), but there was no significant interactive diet×flight effect on dry lean mass ($F_{2,107}$=0.004; P=0.996). Absolute lipid mass (Fig. 3B) was affected by diet ($F_{2,107}$=7.962; P=0.001) and by flight ($F_{1,107}$=29.372; P<0.001) but not by their interactions ($F_{2,107}$=0.130; P=0.878). There were significant main effects of diet and flight on mass-corrected lipid content, but no interactive effect (2-way ANCOVA: $F_{2,106}$=0.130; P=0.879). Body lipid content was higher in locusts eating lower p:c ratio diets ($F_{2,106}$=12.676; P<0.001) and flight decreased lipid content relative to levels in the control groups ($F_{1,106}$=23.845; P<0.001) (Fig. 3).

As predicted, locusts reared on low protein, high carbohydrate diets (14p:28c) had the longest flight duration and quality (Fig. 2). This result corroborated studies with the Mongolian locust showing that a 14p:28c artificial diet increased flight up to 120 min and that 120 min of flight increased carbohydrate consumption in migratory locusts, *L. migratoria* (Cease et al., 2017; Raubenheimer and Simpson, 1997). Lipids are the primary fuel for long distance flight in locusts (Jutsum and Goldsworthy, 1976; Weis-Fogh, 1952). We found that the high carbohydrate diets increased body lipid content (Fig. 3B,C) and that flight decreased body lipid content for all diet groups (Fig. 3B,C). Overall, these results support the hypothesis that lipid stores are critical for promoting flight duration and quality.

Despite the general link between high lipid stores and long-duration flight, our results and other studies suggest that lipid reserves are unlikely to be the only limiting factor for prolonged flight duration, unless lipid stores are particularly low. In our study, even locusts eating the lowest carbohydrate diet likely had sufficient lipid reserves to support 12 h of flight, if 100% of stored lipids can be used. We estimated that locusts eating high protein diets had 116 mg of lipid stores prior to flight; when they stopped after 5.5 h of flight, they still had ∼75 mg of lipid (Fig. 3B). Similarly, male and female migratory grasshoppers (*Melanoplus sanguinipes*) ended flight with significant amounts of lipids stores (Rankin and Burchsted, 1992), suggesting that either not all of the lipid stores are available for use or that some other factor causes locusts to stop flying.

One possible explanation for cessation of flight, consistent with the lower flight duration of locusts fed on low carbohydrate diets, is that flight ceases when carbohydrate levels fall below a threshold. In one study of *L. migratoria*, hemolymph carbohydrate concentration decreased by half in the first 30 min of flight, but then stayed constant for 5 h, during which fat body glycogen stores fell by more than half (Jutsum and Goldsworthy, 1976). These data suggest that flight for 12 h could exhaust glycogen stores, leading to a fall in blood carbohydrate levels and flight cessation. Although lipid is believed to be the primary fuel during long-term locust flight (Pener and Simpson, 2009; Weis-Fogh, 1956), maintaining a relatively high hemolymph carbohydrate content could be necessary to maintain levels of intermediates of the TCA cycle (Sacktor and

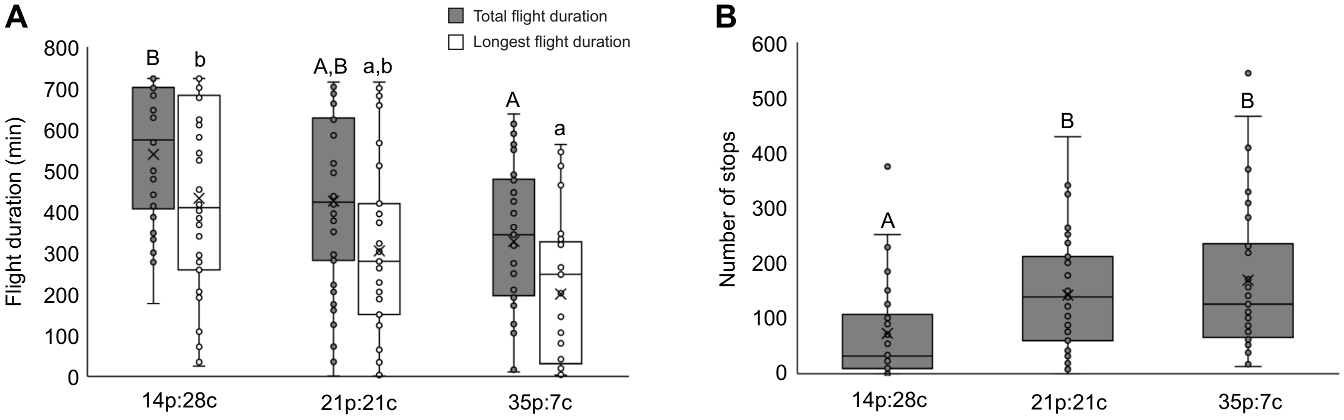

Fig. 2. Flight performance of locusts was affected by relative availability of macronutrients. (A) Total flight duration and longest flight duration increased with an increase in the carbohydrate ratio in the diet. (B) The number of stops during flight was lower in the locust group that consumed a diet with the highest percentage of carbohydrate. Groups with the same letters did not differ significantly. Medians and interquartile ranges are represented by the boxes and center line; crosses indicate means and individual data points are represented by open circles. p:c, protein to carbohydrate ratio.

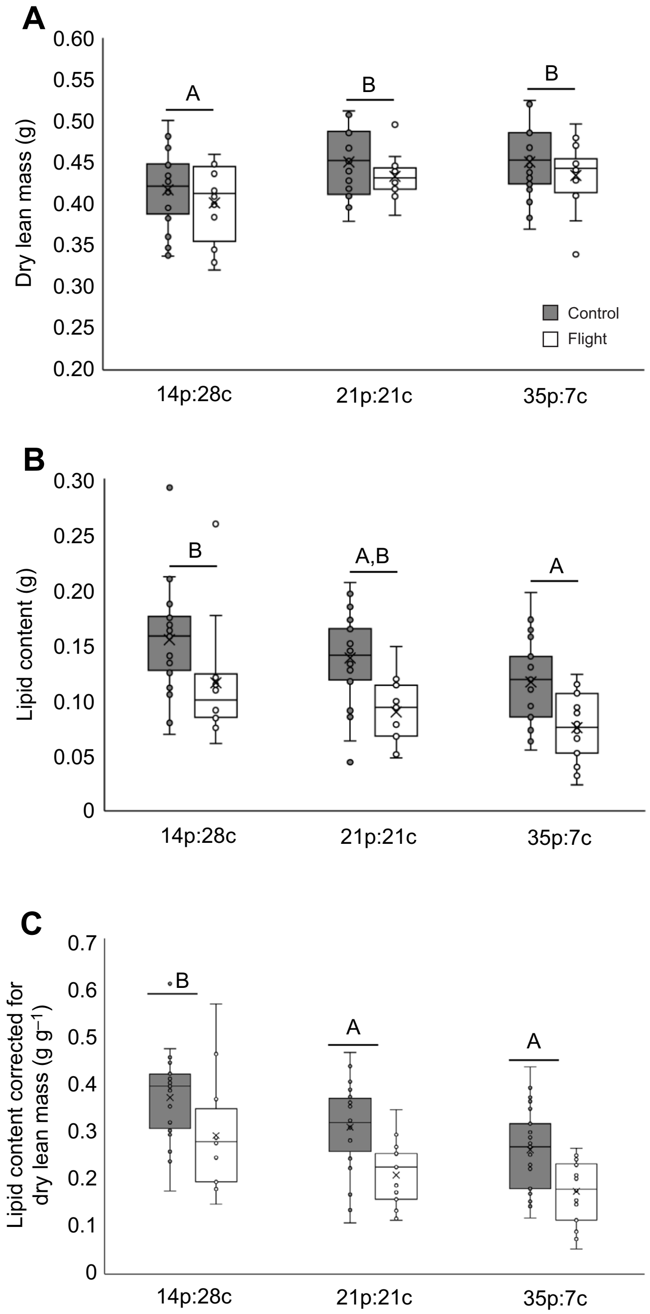

Fig. 3. The effect of dietary macronutrient ratio on pre- and post-flight body lipid content. (A) Lean dry mass was lower in locusts fed a high percentage carbohydrate diet. Total body lipid mass (B) and body lipid content (corrected for dry lean mass) (C) increased with an increase in dietary carbohydrate in the locust diets. Groups with the same letters did not differ significantly. There were no diet×flight interactive effects on these three variables.

Wormser-Shavit, 1966). Additionally, some vital organs such as the brain may require carbohydrate as a metabolic fuel (Jutsum and Goldsworthy, 1976). Rearing locusts on the low carbohydrate diet treatment (35p:7c diet) together with prolonged flight might cause an earlier carbohydrate deficiency, which could in turn, cause an earlier termination of flight.

Another possibility is that flight ceases because of damage. Active muscles, especially insect fight muscles consume high amounts of oxygen (Weis-Fogh, 1967) and produce significant amounts of reactive oxygen species (ROS), which can cause oxidative damage to active muscle tissue (Costantini et al., 2007; Du et al., 2022). There is some evidence that birds must cope with oxidative damage during stopovers (Eikenaar et al., 2020) and that they select fruits with high antioxidant contents (Alan et al., 2013). Similarly, gregarious locusts, which are better flyers than solitarious locusts, have higher antioxidative capacity in their flight muscles (Du et al., 2022). Sugar water fed hawk moths showed less oxidative damage in their flight muscle compared with unfed controls. Sugar-fed moths increased pentose phosphate pathway flux to regenerate NADPH and glutathione, which decreased oxidative damage of fight muscles (Levin et al., 2017). It could be that high carbohydrate diets provided some protection against ROS in our study, allowing locusts to fly for longer.

A third possibility is that flight is terminated owing to water stress, as carbohydrates aid resistance to water stress. Catabolism of glycogen releases ∼2.5 times its dry mass in water (Gibbs et al., 1997). The ambient conditions of our flight experiment (34°C, ∼30% RH) meant the flying locusts likely had a negative water budget (evaporative water loss was predicted to be higher than metabolic water production), as calculated by Weis-Fogh (1967). Plausibly, decreased amounts of body glycogen stores due to low carbohydrate consumption could decrease body water storage (Gibbs et al., 1997) and cause early desiccation and flight termination.

Conceivably, the longer flight duration of locusts fed high carbohydrate diets might be related to changes in flight muscle energetics. Alternative splicing of troponin-t (Tnt) (Marden et al., 2008) and heavy chain myosin (Li et al., 2016) can be affected by nutrition (Marden et al., 2008), and these can alter the power output and energy cost of flight (Marden et al., 1999). In the current study, we showed that low protein (high carbohydrate) diets caused locusts to have ∼8% lower lean dry body weight, so these locusts may have smaller flight muscles with different troponin-t and myosin heavy chains. If the low protein, high carbohydrate locusts used less energy during flight, this may have allowed them to fly for a longer duration if flight termination is linked to a fall in carbohydrate or lipid levels below a threshold, or if flight muscle damage is linked to flight metabolic rate.

Insects are often overlooked but can be an excellent model for exercise physiology research (Wegener, 1996). Insects use the same metabolic fuels and pathways (glycolysis, TCA cycle, β-oxidation and more) as vertebrates, and many genomic tools are available for their study (Cullen et al., 2017; Wang et al., 2014). Here, we show for the first time that consumption of high levels of carbohydrate increases lipid storage and promotes migratory flight. We also uncovered limitations in endurance that are related to nutrition and propose several hypotheses to test the potential mechanisms driving this limitation.

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Competing interests
The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.T., A.J.C.; Methodology: S.T., S.P., G.O.; Validation: S.T.; Formal analysis: S.T., S.P.; Investigation: S.T., S.P., G.O.; Resources: J.F.H., A.J.C.; Data curation: S.T.; Writing - original draft: S.T., G.O., J.F.H., A.J.C.; Writing - review & editing: S.T., S.P., G.O., J.F.H., A.J.C.; Supervision: S.T., J.F.H., A.J.C.; Funding acquisition: A.J.C.

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Data availability

All relevant data can be found within the article and its supplementary information.

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