A GRAIN DIET SUPPLEMENTED WITH INSECTS RATHER THAN FRUITS SUPPORTS A MORE ROBUST BODY CONDITION IN AN OMNIVOROUS TROPICAL SONGBIRD

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Abstract

1. Omnivores utilise dietary sources which differ in nutrients, hence dietary restrictions due to environmental change or habitat alteration should cause nutrient limitations; and thus, deterioration of body condition if omnivory is obligate. 2. We investigated how the body condition of the Village weaver Ploceus cucullatus (weavers), which forages predominantly on grains, responds to insects and fruits deprivation. 3. Forty wild-caught weavers held in aviaries were fed a combination of grains and fruits, or grains and insects ad libitum for eight weeks. We confirmed diet preference by recording the number of foragers on each diet option per minute for one hour and the amount of food left-over after 3 hours of foraging. Fortnightly, we assessed indices of body condition including body mass, pectoral muscle, and fat scores, Packed Cell Volume (PCV) and Haemoglobin Concentration (HBC). We modelled the number of foragers, food left-over and body condition as functions of diet, while accounting for time (weeks) and sex effects. 4. We confirmed grains as the preferred diet and found that males ate more fruits and insects than females. Weavers fed on grains and fruits lost body and pectoral muscle mass and accumulated less fat than those fed on grains and insects. This effect was sex-dependent: females deprived of insects lost more pectoral muscle mass than males of the same group and males but not females, deprived of fruits accumulated more fat reserve than those deprived of insects. PCV and HBC did not differ between diets but increased over the eight weeks. 5. Weavers are likely obligate rather than facultative omnivores, with insects as being a more nutritive supplement than fruits. We conclude that nutrient limitation arising from environmental change or habitat alteration can impair body condition and affect physiological response to environmental seasonality in other obligate omnivores like the weavers.

INTRODUCTION

Omnivory implies nutrient acquisition from plant and animal sources (Agrawal & Klein, 2000; Coll & Guershon, 2002; Singer & Bernays, 2003). Dietary sources utilized by omnivores may differ widely in nutrient content and despite foraging different food types, many omnivores have a primary or preferred diet. For example, most avian omnivores are granivorous, frugivorous or herbivorous species that incorporate protein-rich insects into their diets to complement their protein-deprived primary plant diets (Coll & Guershon, 2002; Burin et al., 2016). Others are diet specialists or facultative omnivores which do not necessarily require supplementation (Griffith et al., 2021). Where omnivory is obligate, deprivation of supplementary diets will lead to nutrient limitation (Gillespie & McGregor, 2000; Gillespie et al., 2012), whereas facultative omnivores may be unaffected by such deprivation (Trichilo & Leigh, 1988; Milne et al., 1996; Milne & Walter, 1997).

Anthropogenic/natural environmental changes which may alter the availability of specific food types can lead to nutrient limitation with effects on body mass maintenance (Krieger et al., 2006; Pap et al., 2008; Nwaogu

et al., 2019; Filipiak & Filipiak, 2020), muscle and fat reserves (Pierce & McWilliams, 2004; Van den Burg, 2009) and physiological parameters such as Packed Cell Volume (PCV) and Haemoglobin Concentration (HBC) (Pyke *et al.,* 2012). For example, a protein-rich diet including insects supports the maintenance of body form and function. Dietary protein deprivation may thus lead to the breakdown of protein-rich tissues including muscles and digestive organs (Piersma & Gill, 1998; Krieger *et al.,* 2006). The ability of animals to temporally adjust body reserves in response to breeding and changes in environmental condition (Likness & Swason, 2011; Petit & Vezina, 2014; Nwaogu *et al.,* 2017; Vezina *et al.,* 2020; Eikenaar *et al.,* 2021) may also be impaired by diet or nutrient limitation with effects on survival and fitness (Cook *et al.,* 2004; see Harrison *et al.,* 2011 for a review). Also, the effects of nutrient limitation may be sex-specific because of differences in breeding roles (e.g., Mallory *et al.,* 2008), physiology (e.g., Filipiak & Filipiak, 2020), and morphology (e.g., Fernández-Montraveta & Moya-Larano, 2007).

In the absence of diet restriction, animals may face nutrient limitations in nature due to changes in the quality of their preferred diet (see Agrawal *et al.,* 1999; Agrawal & Klein, 2000; Bravo *et al.,* 2019), the energetic demand of cold condition (Swanson, 2010), and the occurrence of other energy/nutrient demanding periods of the annual cycle such as breeding and moult (Murphy & Pearcy, 1993; Cherel *et al.,* 1994; Klaassen, 1995). This may lead to temporal over-exploitation of body reserves (Milenkaya *et al.,* 2013; Ndlovu *et al.,* 2017; Andersson *et al.,* 2018; Awoyemi, 2020). To maximize nutrients intake during periods of limited nutrient availability, animals may shift between diets or show preference for a given food type (McWilliams *et al.,* 2004; Lamperti *et al.,* 2014; Kwiecinski *et al.,* 2017) with sex-specific variation in diet preference due to differences in morphology (Walker *et al.,* 2014; Bravo *et al.,* 2019), physiology, and breeding role (Kwiecinski *et al.,* 2017; Treidel *et al.,* 2021).

In birds, body mass, pectoral muscle and fat scores indicate physical condition in terms of energy and nutrient reserves (Milenkaya *et al.,* 2013). PCV and HBC on the other hand, are physiological indices which may indicate overall health status (e.g., Garvin *et al.,* 2007). Omnivorous birds in a changing Afrotropical environment are useful surrogates for investigating how diet restriction and/or nutrient limitation due to environmental changes and timing of annual cycle events can influence body condition. The Village weaver *Ploceus cucullatus* is an omnivorous tropical bird found throughout sub-Saharan Africa (Craig, 2010). Its omnivorous foraging behaviour makes it amenable to captive conditions and suitable for experimental diet manipulation. This allowed the effects of nutrient deprivation on body condition to be determined. In the wild, Village weavers exist in large colonies often around water bodies or human settlements, but they thrive well in captivity and are commonly kept as pets (Collias *et al.,* 1986). Village weavers feed predominantly on grains (Collias and Collias, 1970, Collias *et al.,* 1986), but they also forage on insects (Collias & Collias, 1970; Adegoke 1983), and fruits (Lahti, 2003; Yilangai *et al.,* 2014). Males are polygynous. They build nests but nestlings are predominantly fed by females (Collias & Collias, 1970). Male weavers have brighter feathers compared to females especially during the breeding period (Borrow & Demey, 2004).

In this study, we tested the effect of nutrient deprivation on the body condition (body mass, pectoral muscle score, fat score, PCV and HBC) of wild-caught captive Village weavers. First, we determined that grains were the preferred diet of Village weavers, then we tested how preference for grains, insects and fruits may vary over time and between sexes. We expect weavers to show preference for grains compared to fruits and insects during periods of higher energy demands such as under colder environmental conditions. We also expected diet preference to vary between sexes due to their differences in plumage colouration, sex-roles and physiology. Secondly, we compared body condition indices between male and female weavers fed on grains and fruits and those fed on grains and insects over eight weeks. We expect; a deterioration of body condition in weavers on both diet treatments if omnivory is obligate, and a more pronounced deterioration in weavers deprived of the more essential supplementary diet between insects and fruits. We expected differences in how body condition varies over time and between sexes if nutrient demands vary differently between sexes with changes in environmental conditions over time.

MATERIALS AND METHODS

Experimental set-up

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We trapped 20 male and 20 female adult Village weavers using mist nets around the A. P. Leventis Ornithological Research Institute's (APLORI) Amurum Forest Reserve (AFR) (09deg 87' N, 08deg 97' E), Nigeria between October and November 2020. Each bird was fitted with a uniquely numbered metal ring and a combination of three colour rings. Birds were housed in groups of 10 of equal sexes in four adjacent outdoor aviaries at the APLORI. The aviaries measured 3 x 1 x 2 m with a concrete floor, a metal frame, wire mesh, and a thatched roof made from grass mats. Birds were fed grains, insects, and fruits for two weeks before the commencement of the experiment which lasted a further eight weeks. Birds were randomly assigned to aviaries and diet treatments were assigned to aviaries systematically; with each set of two adjacent aviaries having alternate diet treatments. Birds in two aviaries were fed crushed grains and fruits, while the other two were fed crushed grains and insects. 200 g of each food types were provided in separate trays placed side by side. Food and water were provided *ad libitum* . All birds were weighed (+-0.1 g), scored for pectoral muscle and fat, and sampled for blood to measure PCV and HBC before the diet restriction commenced. Subsequently, birds were sampled fortnightly over 8 weeks. Sampling took place on two consecutive days during each session, with two aviaries of alternate diet treatments sampled per day in a rotating order (Nwaogu *et al.,* 2020).

Diet composition

The grain diet consisted of grass seeds (e.g., Red grass *Themeda triandra* , Rhode grass *Chloris gayana,* Guinea grass *panicum maximum,* and Love grass *Erasgrostis tenella*) available to Village weavers in the wild and crushed cultivated grains (e.g., Pearl millet *Pennisetum glaucum* , Sorghum *Sorghum bicolor* , Maize*Zea mays* , and Rice *Oryza sativa*). The insects' diet consisted of crushed air-dried grasshoppers and immobilized ants, grasshoppers, and termites caught in the AFR using sweep nets in known foraging patches used by Village weavers. The fruit diet consisted of ripe fruits of Common lantana *Lantana camara,* Sumach plant*Rhus natalensis,* Pawpaw *Carica papaya* , and Watermelon*Citrullus lanatus* .

Relative diets preference

We recorded the number of birds feeding on a given food tray at every 60 seconds interval across the four aviaries within an hour with a telescope stationed 25 m from the aviaries. We carried out observations in the morning (1000 – 1100 hrs. GMT) and evening (1600 - 1700 hrs. GMT) of three selected days per week. We recorded the identity and sex of foraging individuals throughout the experiment. Also, we weighed (+-0.1 g) the amount of food left on each food tray (defined as giving up density, hereafter GUD) three hours after food was provided using a digital weighing scale. We measured GUD at 0900, 1200, and 1500, 1800 hours for food provided at 0600, 0900, 1200, and 1500 respectively.

Diets effects on body mass, pectoral muscle, fat, PCV, and HBC

We sampled birds randomly per aviary between 0600 hrs. and 1000 hrs., and returned them together after the last bird had been sampled from a room during each sampling session. Birds were held in soft dark cloth bags after capturing from the aviary and after sampling to minimize stress (Nwaogu *et al.,* 2020). We weighed each bird with a digital weighing scale and scored pectoral muscle and fat on a scale of 1-3 and 0-9, respectively (Redfern & Clark, 2001). We collected 75 µl of blood from each bird into a heparinized micro-haematocrit tube after puncturing the brachial vein with a needle. The blood sample was then emptied into ethylenediaminetetraacetic acid (EDTA) bottle, stored on ice, and transported to the National Veterinary Research Institute (NVRI) Vom, Plateau State, Nigeria for determination of PCV following methods describe by Turkson & Ganyo (2015). To measure the HBC of each bird, micro-haematocrit tube was filled with 10 µl of whole blood and dropped on the strip of a portable handheld haemoglobinometer and the HBC (g $^{-1}$dl) was recorded.

Statistical analyses

All analyses were carried out using the statistical package R version 4.0.2 (R Development Core Team 2020). Data were tested for normality and homogeneity of variance using the Shapiro-Wilk normality test and residual plots respectively. Only the number of weavers foraging per diet per minute deviated from a normal

distribution. To model relative diet preference, we built a generalized linear model with a Poisson error structure including diet, week, feeding session, sex and their two-way interactions as explanatory variables for variation in the number of weavers foraging on each diet per minute. We tested for differences in GUD between diets using a linear model. Diet, week, feeding session (time of day), and their two-way interaction terms were included in the model as explanatory variables for variation in GUD. To test the effect of diet restriction on body condition, we accounted for the effects of moult and aviaries on all indices by including moult status and aviary as predictor variables in the model for each body condition index. The explanatory power of both moult and aviaries on variation in all indices were not significant and so were dropped from all our models. Hence, we built linear models for each body condition index with diet, week, sex, and their two-way interactions as the main explanatory variables. For all models, a post hoc test was used to determine which groups differed significantly from each other.

RESULTS

Diet preference

Grains were most preferred by weavers throughout the eight weeks of the experiment followed by fruits and then insects. The number of birds foraging on fruits versus insects differed significantly only at week five while fruits versus grains differed significantly except in week 5 (Fig. 1A, Table 1 & Table S1). More males foraged on fruits and insects than females, but sexes foraged similarly on grains (Fig. 1B, Table 1 & Table S1). Insects had the highest GUD throughout the eight weeks followed by grains and fruits (Fig. 1C), but the GUD of fruits was only significantly lower than grains in weeks 1 and 4 (Fig. 1C, Table 1 & Table S2).

Effects of diet on body condition

The weavers which fed on grains and fruits significantly lost more body mass between week 0 (before diet restriction) and week 8 (at the end of diet restriction) compared to the weavers that were fed on grains and insects (Fig. 2A, $F_{4, 183}$ = 2.63, p = .036, Table 2). This pattern was similar between sexes (Fig. 2B, $F_{1, 183}$ = 1.17, p = .282, Table 2 & Table S3B). Body mass decreased significantly upon diet restriction (between week 0 and week 2) only in weavers fed on grains and fruits, but weavers fed on grains and insects maintained their body masses throughout the experiment (Fig. 2A, Table S3A) and this was similar for males and females (Fig. 2B, $F_{4, 183}$ = 1.29, p = .275, Table 2 & Table S4).

Muscle size was similar between the weavers fed on grains and fruit, and those fed on grains and insects before diet restriction in week 0 (Fig. 3A), but upon diet restriction, the muscle size of the weavers fed on grains and fruits significantly became lower than those fed on grains and insects (Fig. 3A, $F_{4, 183}$ = 8.32, p < .001, Table 2) and this pattern differed marginally between sexes (Fig. 3B, $F_{1, 183}$ = 3.04, p = .083, Table 2 & Table S3B): females deprived of insects lost more pectoral muscle mass than males of the same group. Muscle size decreased significantly after diet restriction in week 6 (t = 6.88, p < .000, Table S3A), and 8 (t = 3.70, p = .010, Table S3A) in the weavers fed on grains and fruits, but weavers fed on grains and insects maintained their muscle sizes throughout the experiment (Fig. 3A, Table S3A). This pattern was similar for males and females (Fig. 3B, $F_{4, 183}$ = 1.76, p = .138, Table 2 & Table S4).

Overall, the fat score was similar between the weavers fed on grains and fruits, and those fed on grains and insects before diet restriction in week 0 (Fig. 4A). After diet restriction, the weavers fed on grains and insects significantly accumulated more fat compared to the weavers fed on grains and fruits (Fig. 4A) but, this was sex dependent (Fig. 4B, $F_{1, 183}$ = 4.26, p = .040, Table 2). As such, fat scores did not differ significantly (t = - 0. 05, p = .000) between diet treatments for females but, males fed on grains and insects accumulated more fat than those fed on grains and fruits (Fig. 4B, t = - 2. 94, p = .019, Table S3B). For both treatments, fat reserve increased after diet restriction from week 2 – 8 and differed between weeks (Fig. 4A, $F_{1, 184}$ = 3.31, p = .012, Table 2 & Table S3A) and this was similar for males and females ($F_{1, 183}$ = 1.30, p = .273, Table 2 & Table S4).

Diet treatment had no effect on PCV ($F_{1, 183}$ = 0.06, p = .808, Table 3), however, PCV increased significantly over the course of the experiment in both diet treatments (Fig. 5A, $F_{4, 183}$ = 12.54, p < .001, Table 3 &

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Table S5) and this was similar for males and females (Fig. 5B, $F_{4, 183} = 0.09$, $p = .986$, Table 3).

Similarly, diet had no effect on HBC ($F_{1, 183} = 0.28$, $p = .597$, Table 2), but HBC increased significantly during the experiment in both diet treatments (Fig. 6A, $F_{4, 183} = 16.34$, $p < .001$, Table 3 & Table S5). This pattern was similar between sexes (Fig. 6B, $F_{4, 183} = 0.09$, $p = .985$, Table 3).

DISCUSSION

We tested the effect of fruit and insect deprivation on the body condition of wild-caught captive Village weavers. First, we confirmed that Village weavers prefer grains compared to fruits and insects as indicated by observed foraging frequencies on diet types per unit time, and GUD. Weavers fed with a diet of grains supplemented with insects lost less body mass, maintained pectoral muscle, and accumulated higher fat reserves during the eight weeks of the experiment compared to those supplemented with fruits. PCV and HBC did not differ between diet treatments but increased over time in both diet treatments.

The observed preference for grains is consistent with existing knowledge that Village weavers are largely granivores despite being described as omnivores (Collias & Collias, 1970; Adegoke, 1983). Grains and seeds are richer in carbohydrates and fatty acids (which are highly concentrated energy sources) than fruits and insects (Korasov & del Rio, 2007; Dimiceli *et al.,* 2007). Therefore, the consistently higher number of Village weavers foraging on grains relative to fruits and insects suggest that a diet of grains is more crucial for maximizing their daily nutrient requirements relative to fruits and insects. However, despite this preference for grains, weavers foraged on fruits and insects because these food items contain specific vitamins and minerals or nutrients such as carotenoids (a source of yellow, red, or orange pigments), and proteins (Linville and Breitwisch, 1997; Bailein, 2002; Walker *et al.,* 2014) which are unavailable in grains. Fruits contain sugar and carotenoids and the latter the probable source of the yellow plumage colour of the Village weaver as in other birds (Ewen *et al.,* 2006; Osinubi *et al.,* 2018).

Relative diet preference may simply indicate the amount of each food item intake, or effort required to meet daily nutrient/energy requirements. For example, judging by the absolute mass of food items consumed based on GUD estimates, the weavers consumed as much fruits as grains weekly, but this was achieved over a shorter foraging time, suggesting that they were much more efficient in handling the fruits diet provided than grains or that they needed more time on grains to obtain their requirement. Note however, that the observed similarity in GUD between grains and fruits might be partly explained by evaporative water loss from the fruits during exposure in the aviaries, so overall, weavers consume more grains that fruits. The lower GUD of insects on the other hand, may simply imply that the weavers only need to feed on a small amount of insects for their daily dietary protein requirements (Karasov & Levey, 1990; Klassing, 1998). Access to water and digestive constraints may also determine how much of a food item is consumed in the wild. For example, grain foraging may be restricted by water availability especially during the dry season (Molokwu *et al.,*2010), but our *ad libitum* provision of water throughout this experiment may have relaxed this constraint and improved the utilization of grains.

Our observation that males fed more on fruits (and insects) than females is consistent with the idea that colourful males target carotenoid rich foods in the wild (Walker *et al.,* 2014). We presume this is because of the differential need for dietary carotenoids and protein to be incorporated in moulting feathers since males are more brightly coloured than females (Borrow & Demey, 2004) and were actively moulting at the time of the experiment. The observed preference for fruits and insects by the males in our study is unlikely due to dominance of males over the females because both sexes fed equally on grains supplied

ad libitum.

Body mass was found to decrease for weavers on both diet treatments. This implies that both diet combinations are not optimal for the Village weavers. The decrease in body mass was more pronounced in the insect-deprived weavers, suggesting that protein deprivation is more detrimental than fruit deprivation. Fat, and muscles including the digestive organs and pectoral muscles account for about 50% and 25% of the total body mass of birds respectively (Lobocha, 2012; Ndlovu*et al.,* 2017). Our results show that body mass loss

in the weavers fed with grains and fruits is unlikely due to fat loss, but due to pectoral muscle breakdown. The weavers increased fat reserves over time during the experiment probably due to decreasing temperature in the study area. The period between Novemebr and February annually is usually characterised by cold-dry spell with temperatures as low as 3°C in the nights and early mornings when birds need to endure starvation. Protein-rich pectoral muscles are part of the non-fat component of body mass which may be broken down to provide amino acids needed for body maintenance, a plausible explanation for the weavers not to lose fat but significantly deplete muscle tissues. Several studies have reported the loss of body mass due to a reduction in the size of digestive organs rather than pectoral muscles in long-distance migratory birds because muscles are needed for long-distance endurance flight (Piersma *et al.,* 1999; Lindstrom*et al.,* 2000; Pierce & McWilliam, 2004; McWilliams & Karasov, 2005; Krieger *et al.,* 2006). On the contrary, weavers in captivity do not need to fly long distances but needed to continue foraging, so would rather deplete pectoral muscles than shrink their digestive tract. Moreover, a longer digestive tract may be needed to properly digest the low nutritive fibrous fruits diet (Jordano, 1987; Al-Dabbagh *et al.,* 1987).

Protein deprivation in the fruit-fed weavers may be exacerbated by moulting requirements but this may not be the case in this study becaue moult status showed no effect on the observed loss of pectoral muscle mass. About 90% of bird feathers are made up of keratin which is composed of amino acids derived from protein (Stettenheim, 2000). During moults, about 25% of protein mass is depleted and the demand for dietary protein increases (McWilliams, 2008). Having no access to dietary protein, the weavers fed on grains and fruits diet may have catabolized their protein reserve to meet up with protein requirements for other tissue repair and maintenance. Moreover, unknown to us, the birds may have arrseted molt due to protein deprivation (Gosler, 1991) since we took note of molt status only at the beginning of the experiment. Females deprived of insects lost more muscle mass than males on the same treatment. It is likely that the larger body size of males influenced the rate at which muscle tissues are depleted since they could have higher protein reserves than females (Piersma, 1984). Furthermore, female weavers are responsibly provisioning nestlings; therefore, the need to compensate for nutrient deficit incurred by nourishing eggs, nestlings, and fledglings with protein-rich diets may increase the protein requirement of the females (Collias & Collias, 1970; Houston, 1998) and thus could result in muscle depletion.

Variation in body fat may be due to environmental conditions over time rather than diet treatment, but diet may have influenced the intensity of fat accumulation in response to environmental change. We found increased fat reserves in the weavers fed on both diet treatments, but the male Weavers fed on grains and insects increased fat reserves more than those fed on grains and fruits. An increase in fat reserves in response to cold temperature has been reported in several species of temperate birds (Goławski *et al.,* 2015; Brodin, 2017). Energy demands for heat production increase with decreasing temperatures (Goławski *et al.,* 2015). Therefore birds must accumulate fat for both energy requirement and insulation during periods of low temperature. The increase in fat reserve might be a response to cold temperatures since birds were held within the cold-dry harmattan period in West Africa (November to February) which experiences massive fluctuations in daily temperature. Similar increases in body fat and mass were observed in Common Bulbuls *Pycnonotus barbatus* held in captivity in the same study area at the same time of year (Nwaogu, 2019). It is unclear why males fed with grains and insects gained more fat than those fed with grains and fruits. The presence of excess simple sugars from fruits is expected to allow *de novo* production and accumulation of fat (Klassings, 1998) as reported for migrant e.g., White-throated Sparrows *Zonotrichia albicollis* (Smith & McWilliams, 2009). Both sexes accumulated fat similarly when fed on grains and fruits, but males accumulated fat more when fed on grains and insects. By consuming more insects than females, the males might have accumulated more fat than females since a combination of grains and insects provided more fat than grains and fruits.

The observation that diet did not affect PCV, but that PCV increased over time regardless of diet treatments suggests that factors other than diets such as humidity, photoperiod, and temperature may be driving variation in PCV (Fair *et al.,* 2007). An increase in PCV can occur when blood plasma that suspends blood cells is used to disperse body heat in response to cold temperature (Dawson & Bortolotti, 1997). This is consistent with the cold temperature during the study period. Similarly, Swanson (1990) and Abelenda *et al.*

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(1993) found PCV to increase as temperature decreases due to the need to increase heat production in cold temperatures (Carey & Morton, 1976). The lack of a diet effect on PCV is consistent with other studies that found no diet-related differences in PCV in American Kestrel *Falco sparverius* (Dawson & Bortolotti, 1997) and House Sparrows *Passer domesticus* (Gavett & Wakeley, 1986). Sex hormones specifically androgens which support sperm production are known to increase the production of red blood cells in male birds (Shahani *et al.,*2009). This may be responsible for the higher PCV in males than females. Variation in PCV and HBC followed the same pattern. This is not surprising because HBC correlates positively with PCV in Passerines (Velguth *et al.* , 2010). Thus, an increase in PCV in response to cold temperature and due to androgen effect in males might have resulted in a corresponding pattern in HBC.

This study demonstrates that seasonal or anthropogenic environmental changes that can alter the availability of different food types (especially insects) can be detrimental to the maintenance of body condition and physiological response to environmental change in the Village weaver which depends on several food sources to meet its daily nutrient requirement and this may be the case for other omnivores. Moreover, omnivores may be more vulnerable to environmental change despite diverse foraging options due to their complex diet combination (Burin *et al.,* 2016).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS CONTRIBUTIONS

S.O.G., S.A.M., T.C.O., and C.J.N designed the study. S.O.G carried out aviary experiments, while M.S.A., T.C.O., and C.J.N., supervised. S.O.G. and C.J.N. analysed data and interpreted results. S.O.G. developed the first draft of the manuscript. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study Will be deposited in Dryad Digital Repository.

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Figure 1: Relative diet preference of Village weavers *Ploceus cucullatus* over 8 weeks of diet treatments; (A) Number of Village weavers foraging on diet types (B) Number of males foraging relative to females on diet types (C) Variation in giving-up density (GUD) (g) between food types. Alphabets above bars indicate a statistically significant difference between groups after post hoc comparisons at p < .05. Boxes show group medians. GUD of fruits and grains is significantly (p < .05) lower compared to insects across weeks while the GUD of fruits is significantly (p < .05) lower compared to grains in weeks 1 and 4 (Table S2).

Table 1: Differences in the number of Village weavers *Ploceus cucullatus* foraging on diet types per minute of observation, and Giving-up density (GUD) (g) of diet types over 8 weeks of foraging.

Number of Weavers foraging on diet type/minute	Number of Weavers foraging on diet type/minute	Nu
Variables	df	Chis
Diets	2	542.
Week	7	54.2
Sex	1	3.11
Session	1	223.
Diets*Week	14	51.7
Diets*Sex	2	35.1
Diets*Session	2	1.86
Week*Sex	7	29.7
Week*Session	7	20.3
Sex*Session	1	0.24

Statistically significant effects are highlighted in bold. Session = time of day.

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Figure 2: Effect of diet treatment on the body mass (g) of Village weavers *Ploceus cucullatus* over 8 weeks of experiment between (A) Diet types (B) Sexes (f = female, m = male). Boxes show group medians. Boxes for each diet with different alphabets are significantly different while different alphabets above boxes for sexes indicates a significant difference between weeks after post hoc comparisons at p < .05.

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Figure 3: Effect of diet treatment on the pectoral muscle size (on a scale of 1-3) of Village weavers *Ploceus cucullatus* over 8 weeks of experiment between (A) Diet types (B) Sexes (f = female, m = male). Both

sexes had higher and similar muscle scores on grains and insects than on grains and fruits diets. Bars with different alphabets are significantly different after post hoc comparisons at p < .05.

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Figure 4: Effect of diet treatment on the fat score (on a scale of 0-9) of Village weavers *Ploceus cucullatus* over 8 weeks of experiment between (A) Diet types (B) Sexes (f= female, m= male). Males differ in their fat score between diets but females do not. *Differences in* Alphabet above each pair of bars indicate a significant difference between weeks *after post hoc comparisons at p < .05* .

Table 2: Comparison of body mass (g), pectoral muscle score (on a scale of 1-3) and fat score (on a scale of 0-9) between Village weavers*Ploceus cucullatus* fed grains and fruits and grains and insects for 8 weeks.

	Body mass (g)	Body mass (g)	Body mass (g)	Body mass (g)	Pectoral muscle score (1-3)
Variables	df	Sum Sq.	f	p	Sum Sq.
Diets	1	10.10	1.33	.250	3.38
Weeks	4	229.00	7.55	**< .001**	4.57
Sex	1	4241.20	558.90	**< .001**	0.72
Diets*Weeks	4	79.80	2.63	**.036**	2.97
Diets*Sex	1	8.80	1.17	.282	0.27
Weeks*Sex	4	39.20	1.29	.275	0.63
Residuals	183	1388.70			16.34

Statistically significant effects are highlighted in bold.

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Figure 5: Effect of diet treatment on the Packed Cell Volume (PCV) (%) of Village weavers *Ploceus cucullatus* over 8 weeks of experiment between (A) Diet types (B) Sexes (f = female, m = male). *Boxes show group medians. PCV did not differ between diets but differed between weeks for both diets and sexes.* Males had higher PCV than females throughout the experiment on both diets. Differences in*Alphabet above each pair of boxes indicate a significant difference between weeks* after post hoc comparisons at p < .05.

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Figure 6: Effect of diet treatment on the Haemoglobin Concentration (HBC) (g^{-1}dl) of Village weavers *Ploceus cucullatus*over 8 weeks of experiment between (A) Diet types (B) Sexes (f = female, m = male). *Boxes show group medians. HBC did not differ between diet treatment but differed between weeks for both diets and sexes.*Males had higher *HBC* than females throughout the experiment on both diets. Differences in *Alphabet above each pair of boxes indicate a significant difference between weeks* after post hoc comparisons at p < .05.

Table 3: Comparison of packed cell volume (PCV) (%) and haemoglobin concentration (HBC) (g^{-1}dl) between Village weavers *Ploceus cucullatus* fed grains and fruits and grains and insects for 8 weeks.

Variables	PCV (%) Df	PCV (%) Sum Sq.	PCV (%) F	PCV (%) P	HBC (g^{-1}dl) Sum Sq.	HBC (g^{-1}dl) f	HBC (g^{-1}dl) P
Diets	1	1.40	0.06	.808	0.73	0.28	.597
Weeks	4	1224.40	12.54	**< .001**	170.37	16.34	**< .001**
Sex	1	239.80	9.82	**.002**	31.92	12.25	**< .001**
Diets*Weeks	4	48.90	0.50	.735	2.77	0.27	.899
Diets*Sex	1	8.60	0.35	.554	0.83	0.32	.573
Weeks*Sex	4	8.50	0.09	.986	0.96	0.09	.985
Residuals	183	4467.30			477		

Statistically significant effects are highlighted in bold.