Performance of Newly Described Native Edible Cricket Scapsipedus icipe (Orthoptera: Gryllidae) on Various Diets of Relevance for Farming

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Abstract A new native edible cricket species, Scapsipedus icipe Hugel and Tanga, has been described in Kenya for the first time. However, there is lack of information on suitable diets and their effects on the developmental time, survival, weight gain, body length, growth index, preoviposition, oviposition, postoviposition, fecundity, egg eclosion period, adult emergence, and longevity of this species, which are prerequisite for large-scale production. In this study, six diets (wheat bran, soybean, fish offal, pumpkin leaf, carrot, and maize meals) selected to vary in protein, carbohydrate, and fat content were evaluated. The developmental time and survival rate of the different life stages varied considerably on the various diets, with the shortest development and highest survival rate recorded when fed wheat bran diet. Preoviposition duration was significantly longer on maize and carrot diets (>10 d) compared with that recorded on the other diets (<8 d). Body weight and body length were significantly influenced by t different diets tested. Females of S. icipe fed on protein-rich diets (fish offal, soybean, and wheat bran) had significantly higher lifetime fecundity and fertility. Female-biased sex ratio was recorded on wheat bran and soybean diets, whereas male-biased sex ratio was recorded on maize and carrot diets. Our findings reveal that the impact of diet quality on the biological fitness parameters of S. icipe and the implication of the results are discussed in light of effective mass rearing of this species.

Key words: edible cricket farming, diet composition, fecundity, growth performance, reproductive fitness

Crickets (Orthoptera: Gryllidae) are one of the most widely farmed insect groups for human consumption as food and/or high-quality protein ingredients for inclusion in livestock feeds in many regions of the world (Hanboonsong et al. 2013, Lundy and Parrella 2015, Ayieko et al. 2016, Homman et al. 2017). They have been raised on an industrial scale in Western countries for decades, primarily for insectivorous pets or animals in captivity (Van Huis et al. 2013). This is because crickets have high feed conversion ratio, short generation time, tolerate high densities, do not undergo diapauses, are generalist feeders, and are not easily affected by diseases (Belluco et al. 2013; Halloran et al. 2016, 2017). Previous research studies have demonstrated that crickets can recover crude protein (CP) and other essential nutrients more efficiently than the mainstream protein sources (Halloran et al. 2017). In addition, cricket farming directly emits a very small fraction of the greenhouse gases (i.e., significantly low ecological footprint; Halloran et al. 2017) and directly requires in order of magnitude less water and land than farmed livestock (Halloran et al. 2017). Thus, crickets are increasingly being considered an attractive, viable, and sustainable alternative to animal

and plant protein sources. However, in Africa, particularly in Kenya, cricket farming for food and feed is a newly introduced venture in the Lake Victoria region (Ayieko et al. 2016, Ekesi et al. 2016), which is an area with a long-standing history of entomophagy (Ayieko et al. 2010, 2012, 2016; Kinyuru et al. 2013). Although the demand for cricket products is increasing drastically (Ayieko et al. 2016, Homman et al. 2017), most of the communities still rely heavily on artisanal, nonsustainable, and noncost-effective seasonal wild harvesting of crickets with unsafe handling and storage practices posing various health hazards and rendering them economically unsustainable (Acuña et al. 2011, Rumpold and Schluter 2013, Kinyuru et al. 2015). Thus, the development of a comprehensive mass rearing protocol with locally available and affordable feeds is crucial if continuous supply is needed to ensure the availability of these valuable proteins. Crickets are known to eat a large range of organic material (Patton 1967, 1978; Kinyuru et al. 2015; Lundy and Parrella 2015; Miech et al. 2016) and can be reared in crowded conditions and prefer temperatures above 20°C (Patton 1967, 1978; Makkar et al. 2014). Although the mass rearing of some cricket species such as Acheta domesticus (L.) (Orthoptera: Gryllidae) has been well documented (Melissa 2014), this technology remains largely unexploited for native species in Kenya and Africa at large. Following a nationwide survey in Kenya to catalogue edible cricket species, a new native cricket species, Scapsipedus icipe Hugel and Tanga, was described (Fig. 1; Tanga et al. 2018). In many occasions, farmers have attempted to use other livestock feeds including chicken feed (Lundy and Parrella 2015, Ayieko et al. 2016, Kipkoech et al. 2017), vegetable materials, and to some extent their own household food source in feeding crickets, but production levels have remained low for untold reasons (Ayieko et al. 2016). The above challenges faced by farmers to mass rear this new cricket species might be attributed to complete lack of knowledge of suitable feeds and the effect of various feeds on the biological fitness parameters of the cricket, which are prerequisites for large-scale production. There is a need to rethink the possible options of rearing this species in a cost-effective way using diets that are readily available, affordable, accessible, and nutritiously balanced. In this study, we test the hypothesis that rearing diets have a significant effect on the growth performance and reproductive fitness parameters of S. icipe, and we discuss the implication of the results in light of effective mass rearing of this species.

Materials and Methods

Scapsipedus icipe Hugel and Tanga Stock Culture A colony of S. icipe was initiated for the first time at the Animal Rearing and Containment Unit (ARCU) of International Centre of Insect Physiology and Ecology (icipe) using 425 juveniles and 366 adult crickets (248 females and 118 males). The wild-caught population of juveniles and adult crickets were transferred separately into transparent Perspex cages (60 cm height × 50 cm width × 60 cm length) with vertically arranged cardboard egg trays to provide refuge for the crickets. Each cage had a rectangular opening (25 cm × 40 cm) made on the top side of the cage (lid) to which a wire mesh was fixed. Two additional openings (20 cm diameter) were also made on the front and back sides of the cage, screened with wire mesh materials to allow for proper air circulation. According to the protocol by Melisa (2014), the crickets were fed a mixture of soybean flour, wheat bran, and maize diets in excess daily. In addition, fresh plant leaves including young maize shoots were also provided regularly. Wet cotton balls with approximately 70% moisture [confirmed using a moisture sensor with two 12-cm-long probes; HydroSenseTM CS620, Campbell Scientific, Inc., Logan, UT] were introduced into the cages to provide water and to serve as oviposition sites for adult crickets. The cotton balls were replaced every 2 d.

The colonies were maintained at 28 ± 1°C, relative humidity (RH) of 65 ± 5% and a photoperiod of 12:12 (L:D) h light cycle. This species of cricket typically undergoes 9–10 molts to maturity depending on the temperature. In the adult cages, the cotton balls were checked daily, and those containing eggs were carefully removed and transferred into 2-liter transparent rectangular plastic containers (21 × 14 × 15 cm; Kenpoly Manufacturer Ltd., Nairobi, Kenya). Thereafter, the containers were placed in a climate-controlled chamber at 30°C with an RH of 70% and a photoperiod of 12:12 (L:D) h light cycle (Parajulee et al. 1993). An opening (14.5 × 8.3 cm) was made on the lid of each container and covered with fine netting organza material capable of retaining emerging nymphs. The newly hatched nymphs were then transferred into Perspex cages as described above and fed powder soybean and maize diets ad libitum. The rearing cultures were monitored daily to record and remove dead crickets. The colony was reared for 8–12 generations before the start of the experiment. Once every 6 mo, wild-caught crickets were reared separately and the young neonates (pinhead crickets) from the F1 generation were transferred to cages holding the newly hatched neonates of the stock culture to maintain the genetic vigor of the colonies and prevent inbreeding depression as well as disease transfer. In addition, cricket populations were kept at similar low densities to avoid stressful crowding effect, which is very common in insect mass production (Sørensen and Loeschcke 2001). Before the commencement of the experiment, the rearing room was maintained at 28 ± 1°C using Xpelair heater: WH30, 3KW Wall Fan Heater, United Kingdom. The RH in the experimental room was maintained at 65 ± 5% using adiabatic atomizer humidifier Condair ABS3 and a photoperiod of 12:12 (L:D) h. The condition of the room was monitored daily using a digital thermohydrometer (Humidity/Temperature Traceable Dew Point Meter–4800CC). From the adult cricket stock colony, eggs (~1 h old) were collected using Petri dishes (9 cm diameter × 1.2 cm height) filled with 70% moist autoclaved wood shavings (saw dust) screened with aluminum wire mesh netting (2 mm2) to avoid cannibalism. According to the method described by Wineriter and Walker (1988), the eggs were individually counted with the aid of entomological tweezers and a moist fine camel's hair brush under stereomicroscope (Leica MZ 125 Microscope; Leica Microsystems Switzerland Limited), fitted with Toshiba 3CCD camera using the Auto-Montage software (Syncroscopy, Synoptics Group, Cambridge, United Kingdom) at magnification of 25× to avoid damage. In total, 3,000 eggs were subdivided into three groups (1,000 each) and transferred into 4-liter transparent rectangular plastic containers (21 × 14 × 15 cm; Kenpoly Manufacturer Ltd., Nairobi, Kenya) containing moist wood shavings (sawdust). The experimental setup was monitored at 6-h intervals daily until eggs eclosion. An opening (14.5 × 8.3 cm) was made on the lid of each container and covered with fine netting organza material capable of retaining emerging nymphs.

Preparation of Experimental Diets Prior to the experiment, two out of the six food substrates: pumpkin leaves (Cucurbita pepo L. (Violales: Cucurbitaceae)) and carrots (Daucus carota sub sp. Sativus L. (Apiales: Apiaceae)) were sourced once from a farmer who practiced organic farming with no chemicals used for insect pest management to ensure that they were free from any pesticide residues. Wheat bran diets (Triticum aestivum L. (Cyperales: Poaceae)) (coarse outer coating of the wheat seed), corn (Zea mays L. (Cyperales: Poaceae)), and soybean (Glycine max L. (Fabales: Fabaceae)) were purchased from a certified stockist in a local market in Nairobi, Kenya. Fish offal of the silver cyprinid (Rastrineobola argentea Pellegrin (Cypriniformes: Cyprinidae)) also known as the Lake Victoria sardine or 'mukene' or 'omena' (i.e., pelagic, freshwater ray-finned fish in the carp family, Cyprinidae from East

Africa) was purchased from the Muthurwa market in Nairobi, Kenya. All the fresh plant materials were chopped into smaller sizes, placed on plastic sheets with moving dry air (28 ± 1°C) at ambient temperature for 2 d using Xpelair heater (WH30, 3KW Wall Fan Heater). Thereafter, the semidried products were oven-dried at 60°C for 72 h to approximately 98% dry matter (DM; ~2% moisture). The dried materials were later passed through a 3-mm sieve in a Münch hammer mill (Münch, Wuppertal, Germany) to ensure that size suitable for incorporation into cricket diets was achieved. Finally, the dried materials were ground into powder, labeled, and each product stored individually in a tightly closed sterilized transparent glass bottle container in a clean cupboard at room temperature until they are needed for further experiment.

Nutritional Analysis of the Experimental Diets We performed proximate analysis of each of the six selected diets to determine the nutritional components. Prior to further analysis of the various diets at icipe, Nairobi, Kenya, all sun-dried samples were ground into fine powder using a blender (MIKA MBLR2999WB, China) for further analysis. DM content of each sample was measured by oven-drying at 100°C for 48 h until constant weight was achieved (AOAC 1990, Pen et al. 2013). CP percentage was determined by using the Kjeldahl method (AOAC 1990). This value was calculated from a product of nitrogen and a constant factor of 6.25, i.e., nitrogen × 6.25 (Finke 2007). The ash content was determined using a muffle furnace with samples subjected to 600°C for 3 h according to the method described by AOAC (1990). The organic matter was determined by subtracting ash content from 100. The neutral detergent fiber and acid detergent fiber were analyzed with the Velp fiber analyzer (FIWE 6; VELP Scientifica, Usmate Velate, Italy) using reagents described. Velp solvent extractor (SER 148/6) was used to determine fat content (crude fat) with ethyl ether as extractant (AOAC 1990). Gross energy (GE; MJ/kg DM) was calculated as follows: 17.6 + 0.0617 CP + 0.2193 EE + 0.0387 CF − 0.1867 ash, where EE is ether extract and CF is crude fiber (Sauvant et al. 2004). The experiment was replicated three times.

Development and Survival of Scapsipedus icipe Hugel and Tanga At the beginning of the experiment, well ventilated transparent rectangular plastic containers (17 × 12 × 6 cm) were prepared. Seventytwo of these containers served as cages and were allocated to each of the six groups of experimental diets (n = 432). According to the method described by Wineriter and Walker (1988), newly emerged nymphs (pinheads) (~1 h old) were counted with the aid of a fine camel's hair brush under a stereomicroscope and individually transferred into each cage. Each group (72 pinheads) were provided with 1 g of respective experimental diet treatments on an aluminum foil paper (5 × 5 cm), which was replaced after every 2 days. Furthermore, a small vial with a piece of tissue paper placed in the opening to prevent drowning was placed in each cage to serve as a water dispenser. Each experimental setup was then maintained in the thermostatically controlled rearing room described above. The cages were checked daily, and the molted skins recorded until adults. Stage-specific parameters such as developmental time, survival, body length, growth index, and sex ratio were calculated for each diet treatment. Each cage contained a single cricket, which was considered as a replicate (i.e., a total of 72 replicates for each diet treatment).

Body Weight and Body Length Measurement To measure body weight and length of both cricket sexes, 20 newly emerged adults subjected to each food substrate were randomly selected and placed individually in transparent plastic vials (3 cm diameter × 6 cm height) covered with the nylon screen. In each vial, we introduced a 5-h old adult after emergence, closed the lid, allowed ca. 3–5 min for the cricket to settle, and then weighed it using a digital electronic weighing machine with 0.0001 g readability (Kern and Sohn, Ballngen,

Germany). The cricket in the tubes hardly moved when weighed. We recorded the weight for each cricket when the reading on the balance screen did not change anymore. The cricket weight was logged as the total weight minus the tube weight. After weighing, the lengths of each cricket body were carefully measured using a digital Vernier caliper as described by Yoshikazu et al. (2008). We weighed and measured a total of 10 males and 10 females for calculation of the body weight–body length relationships.

Preoviposition, Lifetime Fecundity, Egg Hatchability, and Longevity To determine the effect of each experimental diet on the above parameters, 20 male and female pairs of newly emerged (<24 h old) adult crickets were randomly selected from each diet. Individual pairs of crickets from each group were kept in transparent rectangular Perspex cages (15 × 15 × 15 cm) with openings covered with breathable materials. Each pair of S. icipe from the different diets was provided with water and food ad libitum as described earlier. The cages were observed daily to record the number of eggs laid and mortality. Each cage with paired cricket was provided a Petri dish filled with 70% moist sawdust covered with wire mesh, which served as a suitable oviposition site for the females. The preoviposition period was calculated from the first day of emergence of adult female to the first day of oviposition. The oviposition medium containing the eggs in each Petri dish was emptied and spread on the surface of a light box (Sasco, 2 × 15-WATT 6500K, MODEL 44077 B.S.4533, England) to facilitate the location of eggs. Eggs laid each day per pair of crickets were collected with the aid of a fine wet black camel hair brush and counted using an H-104 Professional Model Japanese Hand Tally Counter—Model 7542. The oviposition devices were replaced daily throughout the lifetime of the crickets. The experiment was terminated when both the female and male died. The effect of diets on egg hatchability and incubation period was evaluated at constant temperature set at 30 ± 0.03°C, 65 ± 5% RH, and 12:12 (L:D) photoregime. Newly laid eggs of S. icipe were obtained daily from the above experiment and placed equidistant into Petri dishes lined with 70% moist black filter paper for each diet tested. Each Petri dish was kept in thermostatically controlled environmental chambers (MIR-554-PE, Sanyo/Panasonic cooled incubators, Japan). EasyLog USB data loggers (EL-USB-2, RH/Temp data logger; MicroDAQ.com, Ltd., 603-746-5524) were placed inside the incubator to record temperature every 15 min. Petri dishes were kept in the controlled chamber, and observations were carried out at 6-h interval until egg eclosion. During observation, egg shells were removed as required with a fine brush and number of hatched eggs recorded. Incubators were regularly monitored and experiments in which temperatures fluctuated more than ±0.03°C were discarded. Statistical Analysis Two-way analysis of variance (ANOVA) was used to test the effect of diet, sex of cricket, and diet × sex interaction on developmental time, body length, and body weight, whereas one-way ANOVA was used to test the effect of diet on reproductive fitness parameters, namely, preoviposition time, oviposition time, and postoviposition time. Data on egg hatchability (as percentage) and on nymph survival percentage were subjected to arsine square root transformation (to stabilize variance) prior to one-way ANOVA. Student–Neuman–Keul's test was used to separate means. Linear regression model was used to examine the relationship between body weight and body length, body weight and longevity, body length and longevity, and body weight and egg load, where diet was included in the regression model as main effect and interaction with the quantitative explanatory variable to test whether the linear relationship between the stated quantitative variables differ with diet. Such a regression model is used to evaluate if the diet regression lines have same slopes (parallel lines) or different slopes (separate lines). All statistical analyses were implemented using R version 3.3.3 (R Core Team 2013).

Results

Diet Nutrient Composition Wheat bran and fish offal diets had the highest GE and crude lipid content, whereas maize meal had the least. Carbohydrate was twofold higher in maize and carrot meals when compared with wheat bran, soybean, and pumpkin leave diets. Estimated CP content of the different diets ranged between 7.4 and 56% with fish offal and soybean recording the highest values, and the lowest value was recorded in maize and carrot diet. DM content ranged between 82 and 93% across the diets (Table 1).

Development and Survival of Scapsipedus icipe Hugel and Tanga The developmental time of the different nymphal stages of S. icipe fed on different diets is summarized in Table 2. The developmental time of S. icipe life stages fed on different diets varied significantly [N1 ($F = 74.7$; $df = 5, 409$; $P < 0.0001$); N2 ($F = 325.9$; $df = 5, 368$; $P < 0.0001$); N3 ($F = 542.8$; $df = 5, 348$; $P < 0.0001$); N4 ($F = 1075$; $df = 5,342$; $P < 0.0001$); N5 ($F = 1094$; $df = 5,335$; $P < 0.0001$); N6 ($F = 992.9$; $df = 5,329$; $P < 0.0001$); N7 ($F = 794.9$; $df = 5, 328$; $P < 0.0001$); N8 ($F = 162.0$; $df = 5,317$; $P < 0.0001$)]. Carrot and maize meals recorded the longest developmental time in all stages N1–N8. The interaction effect Diet × Sex on developmental time of preadults was significant ($F = 4.8$; $df = 5, 312$; $P < 0.0001$). The longest developmental time was recorded on males fed maize meal and females fed fish meal. Shortest developmental time was observed for both male and female preadults fed on wheat bran (Table 2). The survival rate from the first nymphal stage to adult S. icipe varied significantly ($F = 27.1$; $df = 5, 42$; $P < 0.0001$) across the different diets (Fig. 2). The percentage survival of the immature life stages to adult ranged between 45.8% on maize diet to 93.1% on wheat bran diet.

Growth Index, Adult Body Weight, and Body Length of Scapsipedus icipe Hugel and Tanga Of the six types of diets evaluated, the wheat bran diet was more suitable for insect growth with a growth index of 1.4, followed by soybean-based (1.3) and pumpkin leaf-based diets (1.3). The growth index for nymphs that developed on the maize-based diet was about 29.6% lower than that for nymphs that developed on the wheat bran-based diet (Table 3). The performance of the six diets in terms of wet weight of S. icipe did not depend on the sex of cricket as evidenced by the nonsignificance of the interaction term Diet × Sex in the ANOVA ($F = 1.2$; $df = 5, 108$; $P = 0.32$). However, the females (averaged over the diets) weighed significantly higher than the males (averaged over the diets; $F = 37.2$; $df = 1, 108$; $P < 0.0001$). Similarly, the main effect of diet was significant ($F = 42.6$; $df = 5, 42$; $P < 0.0001$). The highest wet weight was recorded when S. icipe was fed wheat bran-based diet and soybean diet for both sexes, whereas the lowest value was recorded on carrot- and maize-based diet. The body length of males and females when fed on the six diets followed a similar trend to that of the wet weight (Table 3). Adult body weight and body length were significantly linearly related in both sexes and the line slopes significantly differed between diets (female: $F = 226.9$; $df = 11, 48$; $P < 0.0001$, $R2 = 0.97$ and male: $F = 53.19$; $df = 11, 48$; $P < 0.0001$, $R2 = 0.92$; Figs. 3a and 4a, respectively).

Reproductive Performance of Scapsipedus icipe Hugel and Tanga The preoviposition ($F = 49.3$; $df = 5, 54$; $P < 0.0001$), oviposition ($F = 117$; $df = 5, 54$; $P < 0.0001$), and postoviposition ($F = 761.1$; $df = 5, 54$; $P < 0.0001$) period varied significantly across the different diets. The longest preoviposition period of 11.1 d was recorded on maize-based diets and the shortest was 5.1 d on fish offal-based diet (Table 4). The preoviposition period did not differ significantly when S. icipe was fed on wheat bran-, soybean-, and fish offal-based diets (Table 4), as well as between carrot- and maize-based diets. Female S. icipe mated as early as day 2 after emergence into adult and oviposition began on day 5 when fed on fish offal diet. Egg production began on day 5 at the rate of 26 eggs per day on fish offal and then

continued at an increasing rate to reach 117 and 116 eggs per day at the middle of egg laying period for soybean and wheat bran, respectively, before decreasing thereafter until death of the cricket (Fig. 5). The oviposition period did not differ when S. icipe was provided with wheat bran, soybean, and fish offal diets, as well as between carrot- and maize-based diets. Furthermore, the postoviposition period did not vary significantly between pumpkin leaf-, carrot-, and maize-based diets (Table 4). The postoviposition period was 22-folds higher when S. icipe was fed on wheat bran-based diet compared with maize meal (Table 4). The cumulative egg production per female S. icipe were similar on carrot- and maize-based diets, fish offal- and pumpkin leaf-based diets, as well as on wheat bran, soybean, and fish offal diets (Table 4). Female S. icipe fed on soybean, wheat bran, and fish offal meals were larger and laid significantly more eggs during their life time than those fed on the other diets (Table 5). Because the adult S. icipe body weight and body length were linearly related, we used body weight as the index of body size to determine the effect of body size on female egg load. Indeed, body weight was linearly related with egg load and such relationship significantly varied with diets ($F = 128.1$; $df = 11, 48$; $P < 0.0001$, $R2 = 0.97$; Fig. 3d). Female-biased sex ratio was recorded when S. icipe was reared on wheat bran, soybean, and pumpkin leaf diets, whereas it was significantly male biased on carrot and maize diets (Fig. 6). However, equal proportion of male and female offspring ratio was observed when S. icipe was reared on fish offal meal. Egg eclosion varied significantly across diets ($F = 9.1$; $df = 5, 54$; $P < 0.0001$). The egg eclosion period for female reared on wheat bran and soybean diets was significantly shorter than on the other four diets (fish offal, pumpkin leaf, carrot, and maize diets). Percentage egg hatchability among the different diets ranged between 54 and 94% with the highest values recorded on soybean, wheat bran, and fish offal meals (Table 5). The interaction term Diet × Sex was not significant on adult longevity ($F = 0.12$; $df = 5, 108$; $P < 0.0001$), so too was the main effect of sex ($F = 2.24$; $df = 1, 108$; $P = 0.14$). However, the diets (averaged over sex) were significantly different ($F = 249.5$; $df = 5, 108$; $P < 0.0001$). Highest longevity was recorded on wheat bran meal and lowest on carrot and maize meals. Adult body size and longevity were significantly linearly related in both sexes, and such relationship was significantly different across the diets (female: $F = 124.5$; $df = 11, 48$; $P < 0.0001$, $R2 = 0.97$ and male: $F = 243.9$; $df = 11, 48$; $P < 0.0001$, $R2 = 0.98$; Figs. 3c and 4c, respectively).

Discussion The findings in the present studies revealed that the developmental time of S. icipe varied substantially between the different diets with those subjected to high-carbohydrate-biased diets showing strongly prolonged developmental time (1.5- to 1.6-folds higher). The developmental period was significantly shortened on wheat bran diet with 25% carbohydrate content and 16% CP. This is in accordance with other documented findings on crickets, which demonstrated that house crickets A. domesticus do well on most animal feeds or poultry mashes with 20% CP content sufficiently supporting adequate growth performance (Woodring et al. 1979, Clifford and Woodring 1990). The ability of S. icipe nymphs to complete their development on lowprotein diets (>9% CP) might probably be due to their capacity to regulate their protein intake more intensely than they do with carbohydrate. However, development of S. icipe fed low-protein diets such as maize and carrot clearly shows that they are inevitable more susceptible to insufficient protein quantities. Thus, suggesting that a nutritiously balanced diet is fundamental for faster development of S. icipe. Our observation is similar to that reported by several authors for other omnivores and herbivores (Raubenheimer and Simpson 2003, Simpson and Raubenheimer 2005, Roeder and Behmer 2014). It is important to note that, although

proteins are essential for development (Nash and Chapman 2014), high-protein content in diets have been reported to show slight detrimental effect on survival and reproduction of insects (Robert and Coby 1988, Sentinella et al. 2013), as observed for S. icipe in the present studies. Thus, the prolonged developmental time observed when S. icipe was subjected to pure fish offal and soybean diets in contrast to wheat bran diet might be attributed to the indirect effect of their relatively high-protein contents. Our observation is further supported by Wilkinson (2001) and Cease et al. (2012), who found that, although proteins are very important resources in insect diets, subsisting on pure or higher than optimal level of protein, inevitably results in adversely affecting an insect's growth and development and inducing a fitness cost. However, our results are insufficient to adequately establish such a relationship because other components may also have influenced this parameter, thus further investigation to understand these interactions is warranted. Scapsipedus icipe was able to undergo nine molts, similar to that report by Craig and Woodring (1990) for the house cricket A. domesticus, but the number days to the last molt for A. domesticus was lower (45 d; Craig and Woodring 1990) compared with 66–107 d observed in the present studies. This huge significant difference observed between both species can be attributed to the quality of the diets, rearing temperature conditions, and the species involved (Patton 1978). Our findings are also strongly supported by Friend (1958), House (1961), and Lundy and Parrella (2015), who demonstrated that in insects, protein levels and composition were more valuable because they are the key determinant of feed conversion efficiency. Our data also clearly demonstrated that protein deficits (maize and carrot diets) are more detrimental to S. icipe nymphal survival than carbohydrate deficits. This agrees with several previous reports from Simpson et al. (2005), Thompson and Redak (2000), and Wilkinson (2001) in grasshoppers, caterpillars, and aphids, respectively. Furthermore, survival rate of S. icipe was considered high on all the diets (>80%) tested, with the possible exception of maize and carrot diet (<55%). Similarly, Collavo et al. (2005) in a more recent study also reported an equally low survival rates for the house cricket A. domesticus fed nutrient-poor diets (24–47.5%) as in our study. Low numbers of S. icipe were found to survive on low-protein diets such as maize and carrot diets, which implies that protein was a limiting resource during the nymphal developmental phase. These results are similar to that reported by Nestel et al. (2004) and Nestel and Nemny-Lavy (2008) who demonstrated that diet manipulation to increase protein content was crucial to optimize the mass-rearing process of various insects. Carbohydrates have also been observed to play a very critical role in the survival of various insect species including crickets (Woodring et al. 1988, Stuhl et al. 2011). The longevity of both sexes of S. icipe fed on the low-protein diets (maize and carrot diets) was threefolds lower compared with those fed wheat bran diet, which suggests that they are more sensitive to the lack of protein in adulthood. Contrary to our expectations, males and females responded similarly to protein ingestion and its effect on longevity. In general, males lived slightly longer than females when both were fed on the same protein diets, although no relationship was established between sex and diet quality. Considering the important role of protein for egg production, we expected that females fed on the low-protein diet would live less than males reared under the same conditions, given that previous studies have shown a higher reproductive cost for females than for males and lower female longevity (Chapman et al. 1995, 1998). Our results do not support those obtained by Chapman et al. (1995, 1998), but corroborate with the findings of Chang et al. (2001), where protein affected male and female longevity equally. In our studies, adult female S. icipe were able to maximize both longevity and egg production rate on a single diet, which is contrary to the observation

reported by Simpson and Raubenheimer (2009). The lifespans of both male and female S. icipe are maximized on a low-carbohydrate, high-protein diet, although it is always expected that the ratios would often considerably be different if the blend of nutrition necessary to maximize a female's lifespan, with the blend needed to achieve the optimal female reproductive performance are compared (Lee et al. 2008, Maklakov et al. 2008, Fanson et al. 2009). This is because there is a sexual difference in the trade-off between lifespan and reproduction in females and males; the females require high levels of protein for reproduction (Wheeler 1996), whereas males require low-protein, high-lipid diets to build energy reserves to support them in their search for females (Stockhoff 1993). However, according to Wu et al. (2008), the relationship between carbohydrate concentration and lifespan is not always linear, which partially explains why despite the high-carbohydrate concentration of maize and carrot diets in our experiment, the longevity of both male and female S. icipe remained extremely low compared with the other diets utilized. The discrepancies in the results observed in the present studies can be attributed to the carbohydrate/protein balance, which has been demonstrated to significantly affect the longevity of Teleogryllus crickets (Maklakov et al. 2008, 2009). Although higher carbohydrate concentrations are expected to increase the longevity of S. icipe, the optimal concentration was not measured in the present studies. The diet used had pronounced effects on fecundity, egg eclosion, and egg hatching success, with adult female S. icipe fed on the soybean diet, showing highest fecundity levels, followed by those fed wheat bran diet. Thus, these results are in line with previous findings that protein-rich diets are superior and have the potential to possibly accelerate metabolic processes for increased egg production (fecundity) and cell aging (Soultoukis and Partridge 2016). This implies that earlier fecundity peaks observed for S. icipe fed on the different diets might correspond with shorter lifespans. Earlier egg production in turn resulted in earlier mortality, possibly due to the reproductive cost. Thus, because insect eggs are primarily composed of protein and lipid (Engelmann 1999, Lorenz 2003, Karl et al. 2007), we anticipate that a high demand for these compounds by ovipositing females will be highly required, which explains why soybean, wheat brans, and fish offal were an excellent source of protein for S. icipe. The higher average egg numbers in S. icipe fed soybean diet mainly reflect a much less pronounced reduction in daily fecundity with female age compared with the other groups. The general decline in egg numbers with female age in turn probably reflects the depletion of essential resources (male ejaculate), given that females were mated once throughout their lifespan. This is consistent with documented reports, which demonstrates that female cricket that mate large numbers of times in a lifetime (seven times for Gryllus bimaculatus De Geer and 15 times for Gryllodes sigillatus Walker) gained fecundity and egg hatchability benefits (Sakaluk et al. 2002; Bretman and Tregenza 2005; Gershman 2007, 2010). This is because male ejaculate does contain not only sperm but also prostaglandin precursors (as well as other substances) that stimulate oviposition in females (Loher and Dambach 1989). Thus, further studies to evaluate the direct benefits of female S. icipe mating large numbers of times on fecundity and proportion of fertilized eggs is crucial to maximize their reproductive success. The body weight and body length were significantly linearly related in both sexes, and the line slopes significantly differed between diets. Indeed, body weight was linearly related to egg load, and the relationship varied significantly with diets. Females with larger body sizes (reflecting the nymphal diet regime) had a higher egg production than those with smaller body sizes reared from poor protein-based diets. Furthermore, diet regime significantly affected female egg production. In contrast, both female body size and diet

regime (wheat bran, soybean, and fish offal diets) during adulthood had no effects on egg hatchability. Apart from the effects of diet regimes on fecundity, we found that egg eclosion period also had a marginal effect on egg hatchability. For example, larger females of insects have been noted to have better reproductive performance than their smaller counterparts (Hagen 1962), which is in agreement with our observation in the present study. Size parameters of adult S. icipe were largely dependent on nymphal nutrition, indicating that plastic phenotypes of S. icipe occurred as a result of varying diet conditions. Both male and female S. icipe experiencing protein-rich food abundance during their nymphal stages had larger body size parameters than those that developed under conditions of protein deficiency. Effects of environmental conditions experienced during the nymphal stages on body size and fitness of adult insects have been widely reported in the literature (Dadd 1973, Honěk 1993). Our results are strongly supported by Waldbauer (1968), who has shown that for most insect species, high-protein diets usually result in higher efficiency of conversion of ingested food (Waldbauer 1968) into high-quality body mass. Our studies also corroborate with that of other studies, which indicates that proteinrich insect diet normally translates into larger body size individuals with higher chances of living longer (Sagarra et al. 2001, Kaspi et al. 2002, Doyon and Boivin 2005). In our studies, longevity was similar between the sexes as reported in previous studies (Yang et al. 1994, Vargas et al. 2000). Our results contrast with the report by Mir et al. (2014), who demonstrated that female tephritid fruit flies live significantly longer than males. However, the mechanisms behind these differences between other order of insects, between sexes within a species, and between experimental studies remain largely unclear. The relationship between female size, longevity, and egg load was strongly influenced by the diet type fed to S. icipe; although the nature of these relationships (positive or negative) has never been measured for this species, several studies have shown that it varies from species to species (Bautista et al. 2001, Eliopoulos et al. 2003, Wang and Messing 2003). Indeed, protein dietary supplements have been shown to have positive effects on ovarian maturation, fecundity, and fertility in insects (Jacome et al. 1999, Aluja et al. 2001, Mangan 2003), indicating that dietary protein is a critical component for S. icipe egg production and, consequently, reproductive success. The main findings of this study are that the protein-rich diets significantly increased the sex ratio of S. icipe in favor of females, except for fish offal diets with equal proportion of male and female offsprings. The results on sex ratio recorded on the various diets are extremely important for any successful and efficient mass production system (Orr and Boethel 1990, Ramadan et al. 1995). According to Etzel and Legner (1999), sex ratio should be kept at an optimum level, by ensuring that the diets and ambient conditions are appropriate to the insect species. Diet has previously been shown to affect the reproductive performance of insects (Emre 1988), with increase in amino acid amount in diet resulting in an increase in male emergence (Yazgan 1972). Conclusion The data obtained from the present study have successfully demonstrated the possibilities of mass breeding S. icipe using single food substrate and provide new information for the first time on several lifehistory parameters of this species on various diets composed such as to vary in protein and carbohydrate. The reason for the prolonged nymphal developmental period and poor survival rate when fed maize and carrot diets can be attributed to insufficient protein-based requirements in the diets. This study also shows that there is a linear relationship between body weight, longevity, and egg load of female S. icipe. The fact that longer survival of S. icipe resulted in greater total egg numbers produced shows that there are some requirements in the diets that prolong the lifetime as much as possible. Further refinements are needed in the mass breeding method,

and additional studies will also be needed to determine the full range of temperatures and ideal nutrient ratio to formulate a more successful nutrient-balanced blended artificial diet for substantial improvement of adult S. icipe fecundity for efficient mass production. Thus, this study improves our understanding of the role of diets in the maintenance of S. icipe as food for human consumption and/or inclusion in animal feeds.

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