

# Effects of an introduced, novel prey on diet and reproduction in the diet-specialist European Starling (*Sturnus vulgaris*)

T.D. Williams, A. Cornell, C. Gillespie, A. Hura, and M. Serota

**Abstract:** Diet specialization has important consequences for how individuals or species deal with environmental change that causes changes in availability of prey species. We took advantage of a “natural experiment” — establishment of a commercial insect farm — that introduced a novel prey item, black soldier flies (*Hermetia illucens* (Linnaeus, 1758)), to the diet-specialist European Starling (*Sturnus vulgaris* Linnaeus, 1758). We investigated evidence for individual diet specialization (IDS) and the consequences of diet specialization and exploitation of novel prey on breeding productivity. In all 4 years of our study, tipulid larvae were the most common prey item. Soldier flies were not recorded in diets in 2013–2014; however, coincident with the establishment of the commercial insect farming operation, they comprised 22% and 30% of all prey items in the diets of European Starling females and males, respectively, in 2015. There was marked individual variation in use of soldier flies (4%–48% and 2%–70% in females and males, respectively), but we found little evidence of dichotomous IDS, i.e., where only some individuals have a specialized diet. We found no evidence for negative effects of use of soldier flies on breeding productivity: brood size at fledging and chick quality (mass, tarsus length) were independent of the number and proportion (%) of soldier flies returned to the nest.

**Key words:** insect farming, European Starlings, diet specialization, tipulid, *Hermetia illucens*, breeding productivity, specialist–generalist.

**Résumé :** La spécialisation du régime alimentaire a d'importantes conséquences pour la manière dont les individus ou les espèces réagissent aux changements environnementaux qui modifient la disponibilité d'espèces de proies. Nous avons tiré profit d'une « expérience naturelle », l'établissement d'une ferme à insectes commerciale, qui introduisait une nouvelle proie, la mouche soldat noire (*Hermetia illucens* (Linnaeus, 1758)), pour l'étourneau sansonnet (*Sturnus vulgaris* Linnaeus, 1758), une espèce dont le régime alimentaire est spécialisé. Nous avons examiné les indices de spécialisation du régime alimentaire individuel (IDS) et les conséquences de la spécialisation du régime alimentaire et de l'exploitation de nouvelles proies sur la productivité reproductrice. Pour toutes les 4 années de l'étude, les larves de tipules constituaient les proies les plus fréquentes. Des mouches soldats n'ont pas été observées dans les régimes alimentaires en 2013–2014; cependant à la suite de l'établissement de la ferme à insectes commerciale, elles représentaient 22 % et 30 % de toutes les proies individuelles chez les femelles et les mâles, respectivement, en 2015. Une variation marquée entre individus de l'utilisation de mouches soldats (4 % – 48 % et 2 % – 70 % chez les femelles et les mâles, respectivement) a été notée, mais peu d'indices d'IDS dichotome, c'est-à-dire une situation dans laquelle seuls certains individus ont un régime alimentaire spécialisé. Nous n'avons noté aucun indice d'effets négatifs de l'utilisation de mouches soldats sur la productivité reproductrice; la taille des couvées au moment de l'envol du nid et la qualité des oisillons (masse, longueur du tarse) étaient indépendantes du nombre et de la proportion (%) de mouches soldats rapportées au nid. [Traduit par la Rédaction]

**Mots-clés :** culture d'insectes, étourneau sansonnet, spécialisation du régime alimentaire, tipule, *Hermetia illucens*, productivité reproductrice, spécialiste–généraliste.

## Introduction

Ecological specialization is a key concept in ecology and evolutionary biology and the question of what governs the dietary niche of an animal has long been a central focus of community ecology (Futuyma and Moreno 1988; Devictor et al. 2010). In relation to foraging and diet selection, a long-standing dichotomy has been between generalists, which eat a diverse array of foods, and specialists, which eat only a narrow range of available foods, although these are now generally acknowledged to be ends of a continuum especially among species or among environments (Shipley et al. 2009; Sherry 2016). Bolnick et al. (2003) also chal-

lenged the idea of the traditional generalist–specialist dichotomy by highlighting the fact that individuals within the same species can often have different niche preferences even in the same environment, i.e., they can show individual diet specialization (IDS). Individuals in a single population might express different diet preferences due to genetic differences (e.g., sexually dimorphic morphological feeding adaptations) or because of variation in learned behaviours. Bolnick et al. (2003) summarized a gradient of diet specialization that characterizes the overlap among individuals within populations: (i) totally overlapping diets (pure generalists), (ii) partially overlapping diets (functional specialists), and (iii) non-overlapping diets (pure specialists). More re-

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cently, Pagani-Nunez et al. (2016) proposed that generalists can be divided into (i) facultative generalists, which are able to develop new dietary specializations, and (ii) obligate generalists, which also forage in a broad variety of prey but are unable to develop new dietary specialization.

It has been suggested that the specialist–generalist continuum can also have conservation implications (Bolnick et al. 2003), with diet specialization predicting how individuals or species might deal with environmental changes that might cause changes in availability of prey species (Devictor et al. 2008; Ducatez et al. 2015). In general, a specialist will be most effective in a stable environment by choosing a specific diet that allows it to co-exist with, or outcompete, other species, but will be less effective in a changing environment where it's preferred prey might vary in availability. Although there are many examples of specialist birds that have gone extinct following human-induced changes to the environment (Fitzpatrick and Rodewald, 2016), few examples have been directly linked to changes in prey type. In contrast, facultative generalists might be at an advantage when new prey items appear on the foraging landscape owing to environmental change if individuals can develop (and populations can evolve) novel specializations to preferably exploit alternative resources (Pagani-Nunez et al. 2016).

Although experimental studies have manipulated specific learned behaviours, feeding innovations, and problem solving in relation to foraging behaviour (e.g., Aplin et al. 2015; Lefebvre et al. 2016), it is challenging to manipulate the diet of a species on a landscape scale. Here we take advantage of a “natural experiment” — the establishment of a commercial insect farming operation (<http://www.enterrafeed.com>) — where a novel prey item, black soldier flies (*Hermetia illucens* (Linnaeus, 1758); henceforth soldier flies unless otherwise specified), was suddenly introduced into the breeding diet of European Starlings (*Sturnus vulgaris* Linnaeus, 1758). Commercial insect farms represent another example of human-induced change to the agricultural landscape that could affect farmland- and grassland-dependent bird populations via changes in prey availability (Dossey et al. 2016; Gahukar 2016; Stanton et al. 2018). During the breeding season, European Starlings are thought to be diet specialists (see Discussion) adapted to mainly exploit a single food type (tipulid or similar soil-dwelling larvae), and it has been suggested that this could be a key factor in explaining the patterns of population decline associated with habitat changes that have occurred throughout the original range of the European Starling (Heldbjerg et al. 2016). Our specific objectives were (i) to describe the breeding diet of European Starlings in the 2 years prior to and 2 years after the appearance of soldier flies; (ii) to determine if there was IDS in terms of the extent of exploitation of the novel soldier fly prey; and (iii) to determine the effect of diet specialization (occurrence of tipulid larvae) and exploitation of novel prey (occurrence of soldier flies) on breeding productivity. We initially predicted that if European Starlings were true specialists, then they would not readily use an alternate, novel prey item (soldier flies). However, given our results (see below) and given that soldier flies are energetically less profitable (Bell 1990), we predicted that (i) there would be IDS (sensu Bolnick et al. 2003), i.e., only some individuals would use the new prey source, and (ii) these individuals would have lower chick quality or breeding productivity.

## Materials and methods

Fieldwork was conducted between April and June 2013–2016 on a nest box breeding population of European Starlings at Davistead Dairy Farm, Langley, British Columbia, Canada (49.08°N, 122.37°W). This site comprises ~150 nest boxes mounted on posts and on farm buildings surrounded by mixed agriculture and pasture, with 70–80 boxes used by European Starlings each year. Each year we follow the same basic field protocol (e.g., see Love and

Williams 2008; Fowler and Williams 2015; Williams et al. 2015): nest boxes were checked daily from 1 April to late June, for first and second broods, to determine laying date, egg size, clutch size, and brood size at day 6 after hatching (during peak growth of chicks), and again on day 17 shortly before fledging. We corrected brood size at fledging for any chicks that were subsequently found dead in the nest after fledging at day 21. We recorded body mass ( $\pm 0.01$  g) and body size (tarsus length and wing length;  $\pm 0.1$  mm) at day 17 after hatching. We restrict our analysis to first broods because we obtained insufficient data for second broods, especially for males, for robust analysis. All research was conducted under Simon Fraser University Animal Care permits (Nos. 657B-96, 829B-96, 1018B-96) following guidelines of the Canadian Council on Animal Care and Environment and Climate Change Canada banding permit (#10646).

## Insect prey and diet data

We obtained information on breeding diets of European Starlings feeding chicks in three ways: (1) visual observations of birds returning to the nest with food during our standard provisioning observations; (2) from meals collected from returning adults; and (3) video analysis of birds returning to the nest with food (the latter in 2015–2016 only). We focused on four prey species that comprise the main breeding diet of European Starlings (see Results): crane fly (*Tipula paludosa* Meigen, 1830) larvae, rat-tailed maggots (*Eristalis tenax* (Linnaeus, 1758)), earthworms (*Lumbricus terrestris* Linnaeus, 1758), and (in 2015–2016) black soldier flies. Black soldier fly occurrence and availability was related to the establishment of a commercial insect farming operation 0.5 km from the centre of our long-term study area, directly adjacent to nest box and natural foraging areas used by European Starlings (the insect farm produces sustainably grown products such as high-protein meal and fertilizer from black soldier fly larvae; <http://www.enterrafeed.com>).

Prey data were obtained opportunistically from visual observations during our standard 30 min behavioural (provisioning) observations conducted between 0900 and 1400 PST, 2–3 times during days 6–8 and 12–14 after hatching (for details see Fowler and Williams 2015). We pooled tipulid larvae and rat-tailed maggots as soil larvae, because these could often not be reliable distinguished, and we analysed presence or absence of each prey item (1 or 0) per meal. We collected actual prey from meals brought back to the nest in two ways: (1) neck collaring of chicks (Wright et al. 1998) and (2) nest box trapping of adults using Van Ert traps (Van Ert Enterprises, Leon, Iowa, USA), where adults would typically drop food on the side of the nest when the trap was triggered; both methods were used between 9 and 12 days after hatching.

In 2015 and 2016 only, we obtained diet data from video observations (JVC GZ-R70 Quad Proof HD Camcorder). Nest boxes were videoed for a minimum 30 min on 2–3 different days between days 6–8 and 12–14 after hatching between 0900 and 1400 PST (matching up with visual provisioning observations). Videos were analyzed using VLC Media Player, which allows for pausing or slowing down video playback. Only 30 min of the video were analyzed and the first 5 min were excluded to minimize the effects of disturbance at the nest. For each nest visit by parent birds, we recorded the load size (number of prey) and type of prey. Sex of the provisioning bird was determined by presence of metal or color bands on females. All females were fitted with a radio transmitter (Lotek digitally coded nanotag NTQB-4-2; 2.2 g including leg-loop harness) and some females were wing-clipped by removal of their 2nd, 5th, and 8th primary feathers (as part of another study on experimental manipulation of activity and costs of reproduction; see Results).

All data were analyzed using SAS version 9.4 (SAS Institute, Inc. 2013). Values are presented as means  $\pm$  SE (unless otherwise stated), with significance at  $P < 0.05$  (unless otherwise stated).

## Results

### Annual variation in diet from visual observations and meal collection

Data were available for  $n = 282$  meals identified from visual observations during first broods (2013:  $n = 52$ ; 2014:  $n = 102$ ; 2015:  $n = 91$ ; 2016:  $n = 37$ ). Soil larvae (tipulid larvae + rat-tailed maggots) were the most common prey item being present in >78% of observed meals (i.e., single nest visits) in all 4 years (Figs. 1a and 1b; no significant difference among years,  $\chi^2_{[3]} = 5.25$ ,  $P = 0.15$ ). No soldier flies were recorded in 2013 or 2014, but these were observed in 6.6% and 13.5% of visually observed meals in 2015 and 2016, respectively ( $\chi^2_{[3]} = 17.1$ ,  $P < 0.001$ ; Fig. 1a).

Data were available for  $n = 104$  meals collected by neck collaring of chicks and trapping adults during first broods (2013:  $n = 10$ ; 2014:  $n = 40$ ; 2015:  $n = 18$ ; 2016:  $n = 36$ ). Tipulid larvae were the most common prey item in these meals, but percent presence varied among years: tipulid larvae were present in 80% of meals in 2013 and 2014, but only 50.0% and 55.6% of meals in 2015 and 2016, respectively ( $\chi^2_{[3]} = 8.21$ ,  $P = 0.041$ ; Fig. 1b). No soldier flies were recorded in 2013 or 2014, but these were present in 38.9% and 25.0% of meals in 2015 and 2016, respectively ( $\chi^2_{[3]} = 19.3$ ,  $P < 0.001$ ; Fig. 1b). We identified  $n = 255$  individual prey items from the 104 collected meals (mean = 2.5 prey items/meal; range = 1–11 prey items/meal). Black soldier flies made up 54.7% and 24.5% of all prey items identified in collected meals in 2015 and 2016, respectively. Rat-tailed maggots were present in 12.5% of all meals overall, but they were most common in 2016 (25%) ( $\chi^2_{[3]} = 8.05$ ,  $P = 0.05$ ; Fig. 1b). Worms were present in 23% of all meals (not different among years,  $P > 0.50$ ). Mean ( $\pm$ SD) wet mass of the different prey items was as follows — tipulid larvae:  $25.2 \pm 2.0$  mg ( $n = 96$ ); rat-tailed maggots:  $22.0 \pm 7.3$  mg ( $n = 24$ ); black soldier flies:  $6.0 \pm 2.0$  mg ( $n = 59$ ).

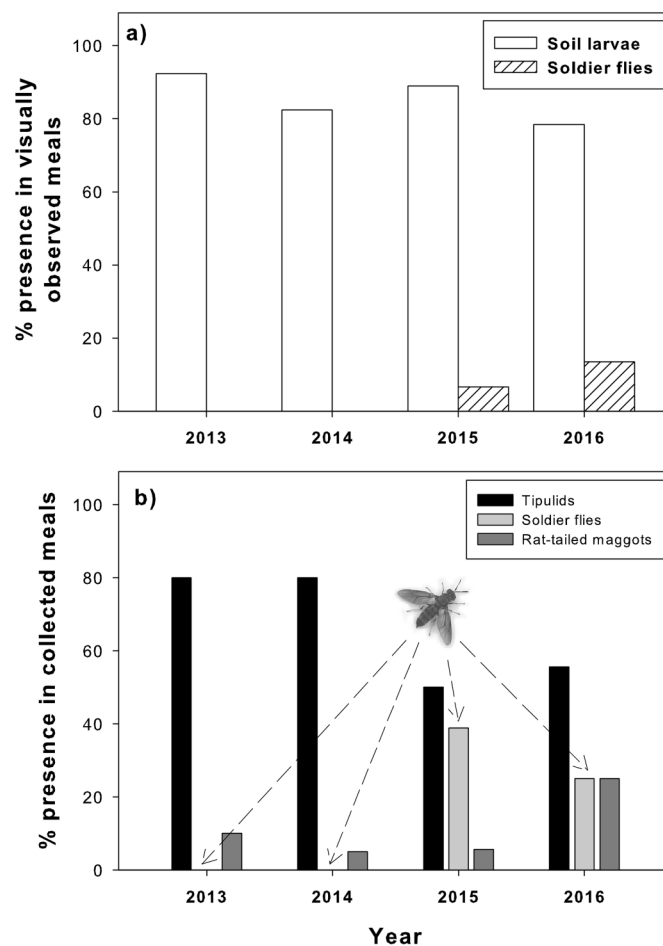
### Variation in diet from video analysis

Data were obtained for  $n = 1388$  individual meals from video analysis of which  $n = 1335$  were single prey type meals and only 45 (3.3%) were multiple prey type meals. For the latter, only one meal contained three different prey types and most meals included tipulid larvae + rat-tailed maggots ( $n = 22$ , 49%) or tipulid larvae + soldier flies ( $n = 14$ , 31%). For simplicity, we restricted subsequent analyses to single prey type meals (96.4% of all recorded meals) representing 2648 individual prey items,  $n = 2033$  prey from females and  $n = 615$  prey from males.

Overall, there was a significant difference in the frequency of main prey items in relation to treatment. Wing-clipped females brought back fewer tipulid larvae (65.4% vs. 73.3%) and more soldier flies (15.1% vs. 12.1%) and rat-tailed maggots (18.1% vs. 13.3%) than females with radios only ( $\chi^2_{[4]} = 16.3$ ,  $P = 0.003$ ). Male partners of manipulated females showed the opposite pattern: males mated to wing-clipped females brought back more tipulid larvae (81.4% vs. 67.6%) and fewer soldier flies (12.7% vs. 26.3%) ( $\chi^2_{[4]} = 19.2$ ,  $P < 0.001$ ). However, there was no effect of treatment on provisioning rate (number of meals/30 min) for either sex ( $P > 0.40$  in both cases) or on breeding productivity (brood size at fledging,  $P > 0.30$ ; mean fledging mass,  $P > 0.70$ ; or fledging tarsus length,  $P > 0.95$ ). Furthermore, individuals in both treatments were evenly distributed in terms of their rank order of frequency of soldier flies in the diet (see Fig. 3). Therefore, for the purposes of this paper, we pooled diet data across treatments for subsequent analysis.

Males contributed less to provisioning compared with females: males accounted for only 21% of meals (283/1335) and 23% of total prey items (615/2648) brought back to the nest ( $n = 36$  nests over 2015–2016). For  $n = 6$  nests, males were not recorded feeding chicks. Mean ( $\pm$ SE) provisioning rate was  $5.77 \pm 0.38$  meals/30 min in females and  $1.70 \pm 0.34$  meals/30 min in males (paired  $t_{[36]} = 7.61$ ,  $P < 0.001$ ).

**Fig. 1.** Annual variation in breeding diet of European Starlings (*Sturnus vulgaris*) for 2013–2016 based on (a) visually observed meals and (b) collected meals that highlight the occurrence of black soldier flies (*Hermetia illucens*) in the diet in 2015 and 2016.



In females, there was significant annual variation in diet composition of food brought back to the nest ( $\chi^2_{[4]} = 412$ ,  $P < 0.001$ ; Fig. 2a). Tipulid larvae were the most common prey item in both 2015 (76%) and 2016 (65%). However, soldier flies comprised 22% of all prey items in 2015 but only 5% in 2016 and, conversely, rat-tailed maggots were not recorded in the diet in 2015 but comprised 29% of prey in 2016. Males showed the same general pattern of variation in diet: composition of food brought back to the nest differed between years ( $\chi^2_{[4]} = 110$ ,  $P < 0.001$ ; Fig. 2b). Tipulid larvae were the most common prey in both years (67%–77%), but males brought back a higher proportion of soldier flies in 2015 (30%) than in 2016 (6%). Conversely, males brought back more rat-tailed maggots in 2016 (16%) than in 2015 (0%).

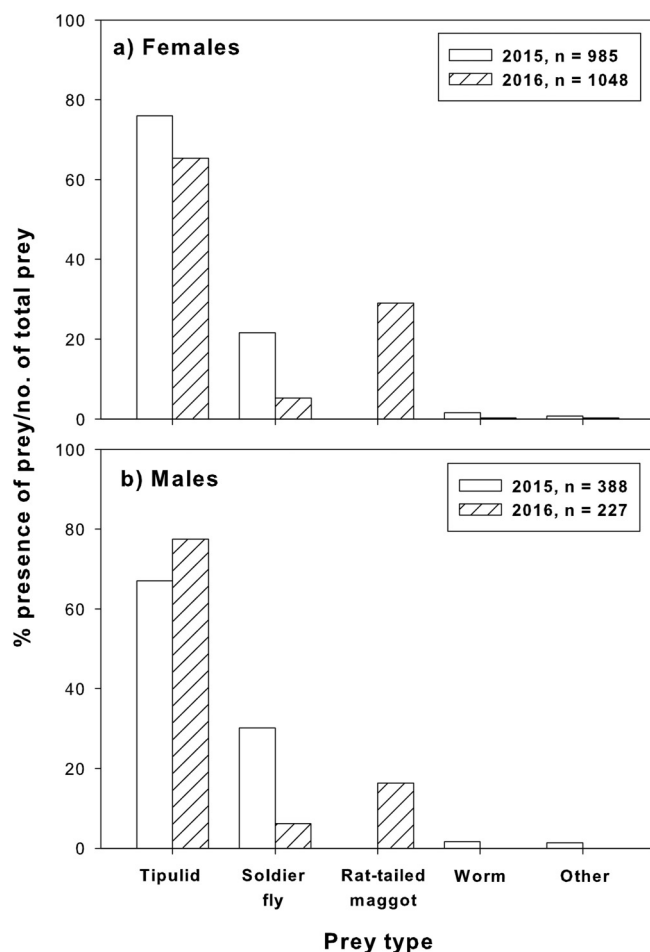
There was marked individual variation in the percentage of soldier flies in the food individual birds brought back to the nest and this varied among years (Figs. 3a–3d). In 2015, every female brought back at least some soldier flies (range = 4.2%–47.7%; Fig. 3a), but in 2016, only 5/19 females had soldier flies in their diet and the maximum percentage was lower (range = 1.9%–26.2%; Fig. 3b). Again, males showed a similar pattern, with 9/15 males bringing back soldier flies in 2015 (maximum = 71.4%; Fig. 3c) and 4/15 males in 2016 (maximum = 28.6%; Fig. 3d).

### Relationship between diet composition and breeding productivity

There was no difference in brood size at fledging for nests where the female's diet contained no soldier flies ( $3.9 \pm 0.3$  chicks)



**Fig. 2.** Annual variation in breeding diet of European Starling (*Sturnus vulgaris*) females (a) and males (b) in 2015 (open bars) and 2016 (hatched bars) from video analysis ( $n$  = total number of prey items).



compared with females whose diet contained soldier flies ( $3.7 \pm 0.3$  chicks;  $F_{[1,34]} = 0.12$ ,  $P > 0.90$ ). Similarly, there was no difference in chick fledging mass ( $71.8 \pm 1.6$  vs.  $75.1 \pm 1.3$  g;  $F_{[1,34]} = 2.58$ ,  $P = 0.11$ ) or chick tarsus length ( $29.9 \pm 0.4$  vs.  $30.4 \pm 0.3$  mm;  $F_{[1,33]} = 1.13$ ,  $P > 0.25$ , controlling for chick mass) comparing females that did not or did bring soldier flies back, respectively. Each of these measures of breeding productivity were also independent of the proportion (%) of soldier flies in food brought back to the nest by females ( $n = 21$ , range = 1.9%–47.7% as above;  $P > 0.49$  in all cases).

The number of chicks at fledging was positively related to the mean number of tipulid larvae ( $F_{[1,34]} = 6.05$ ,  $P = 0.02$ ; no treatment effect or interaction,  $P > 0.50$ ; Fig. 4a) but not the mean number of soldier flies ( $P > 0.60$ ; no treatment effect or interaction,  $P > 0.25$ ; Fig. 4b) returned to the nest/30 min by females. In contrast, chick mass and chick tarsus length were independent of the number of tipulid larvae or the number of soldier flies brought back to the nest/30 min by females ( $P > 0.05$  in all cases).

When we pooled male and female diet data for each nest and analysed breeding productivity and chick quality in relation to food brought back by both parents, brood size was positively related to combined mean number of tipulid larvae returned to the nest/30 min ( $F_{[1,35]} = 7.39$ ,  $P = 0.011$ ; no treatment effect or interaction,  $P > 0.50$ ; Fig. 4c). In addition, there was also a significant positive relationship between brood size at fledging and mean number of soldier flies brought by both parents/30 min ( $F_{[1,21]} = 10.02$ ,  $P = 0.005$ ; no treatment effect or interaction,  $P > 0.60$ ;

Fig. 4d). Chick mass and chick tarsus length were independent of both total number and proportion of tipulid larvae and soldier flies in the combined diet ( $P > 0.10$  in all cases) and brood size at fledging was independent of the proportion of tipulid larvae or soldier flies ( $P > 0.50$  in both cases).

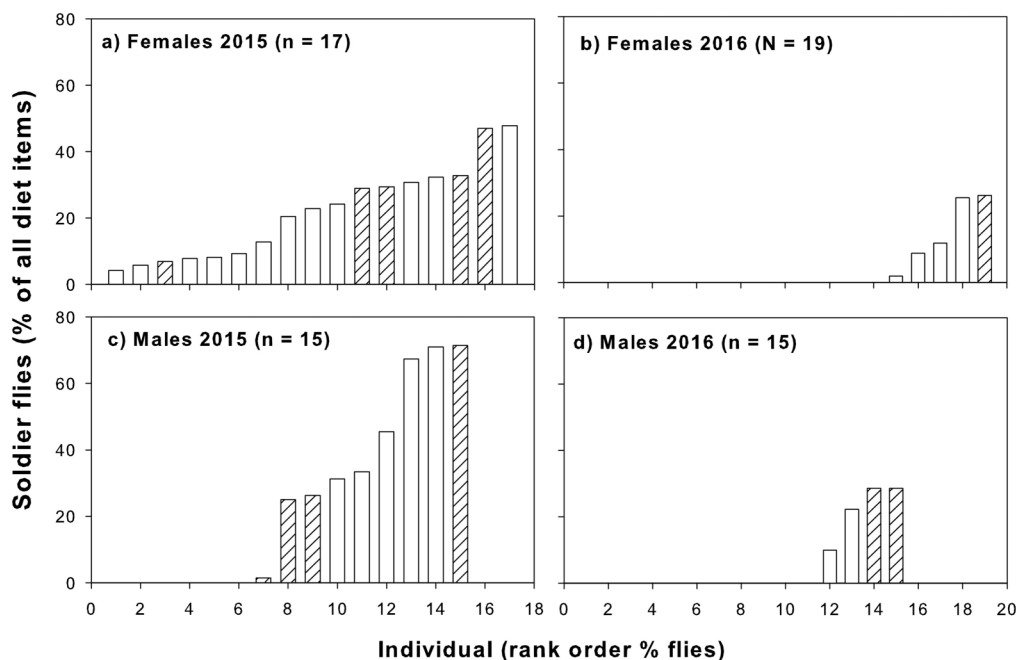
## Discussion

As European Starlings are considered diet specialists, our initial prediction was that they would not use soldier flies once the soldier flies appeared on the foraging landscape. In contrast, European Starlings immediately started including soldier flies in their diet in 2015, coincident with the establishment of the commercial insect farming operation, and every individual female that we sampled included soldier flies in their diet in 2015. There was marked individual variation in use of soldier flies (4%–48% of food items), but this variation was continuous and was consistent with the dichotomous IDS. Use of soldier flies was also relatively transient with only 5/19 females using soldier flies in 2016 (most likely due to better containment of the soldier flies at the commercial facility; see below); this might suggest some level of individual specialization (sensu Bolnick et al. 2003). However, despite quite high and variable use of soldier flies, we found no effect of prey type on chick quality and breeding productivity; breeding productivity was more dependent on the amount of food brought back to the nest rather than the type of prey.

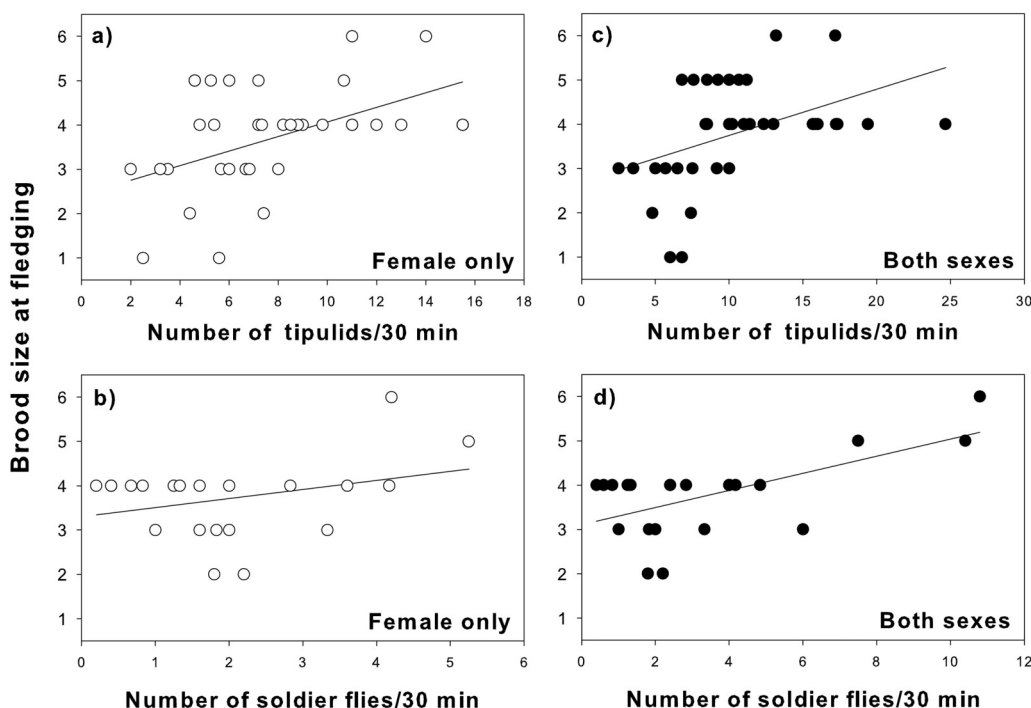
European Starlings are typically considered diet specialists during the breeding season based largely on studies in their native range. Soil-dwelling larvae are taken most frequently in pastures, mown fields, and lawns (Tinbergen 1981; Feare 1984), and tipulid larvae are a key resource for adult European Starlings provisioning their young in their traditional habitat (lowland farmland). Tipulid larvae dominate in the breeding diet in Holland (60% by wet mass: Tinbergen 1981) and in the U.K. (83% by wet mass: Dunnet 1955; 76% by dry mass: Rhymer et al. 2012). European Starlings are an introduced species to British Columbia, as well as the rest of North America, but they also commonly breed in lowland farmland habitat and, at our study site, they use the same tipulid species as in their native range (*T. paludosa* and possibly *Tipula oleracea* Linnaeus, 1758; A. Cornell, unpublished data), which were also introduced in the 1960s (Wilkinson and MacCarthy 1967; Myers and Iyer 1981). Outside of the breeding season, European Starlings can have a much more varied diet especially in fall and winter, including fruits, berries, seeds, livestock feed from feedlots, and human garbage (Cabe 1993). This suggests that European Starlings are functional specialists (sensu Bolnick et al. 2003; Pagani-Nunez et al. 2016) because they are adapted to mainly exploit a single food type or niche during breeding but are capable of exploiting other niches either opportunistically or when primary food is in short supply.

We used three different methods of data collection to determine diets and use of soldier flies: visual observation, meal collection, and video observation. Although each method has some biases, data from each method showed the same overall result. In our study, soil-dwelling larvae (tipulid larvae and rat-tailed maggots) were present in >78% of meals based on visual observations in all 4 years; tipulid larvae were present in 80% of meals collected in 2013 and 2014 and they were the most common prey item in both 2015 (76%) and 2016 (65%) based on video analysis. This is consistent with previous studies (cited above) showing that tipulid larvae are a key resource during breeding. However, our data clearly showed that the breeding diet changed substantially between 2014 and 2015, coincident with the establishment of the commercial insect farming operation on the southwest edge of our study site. Soldier flies were not recorded in diets in 2013 or 2014 (nor in the previous 12 years of our study back to 2002), but in 2015, soldier flies comprised 22% and 30% of all prey items brought to the nest by females and males, respectively, with a correspond-

**Fig. 3.** Individual variation in frequency of occurrence of black soldier flies (*Hermetia illucens*) (rank order % of total prey items) in the breeding diet of European Starlings (*Sturnus vulgaris*): (a) females in 2015; (b) females in 2016; (c) males in 2015; (d) males in 2016.



**Fig. 4.** Relationship between brood size at fledging of European Starlings (*Sturnus vulgaris*) and number of prey returned to the nest per 30 min for (a) tipulid larvae by females, (b) black soldier flies (*Hermetia illucens*) by females, (c) tipulid larvae by birds of both sexes, and (d) black soldier flies by birds of both sexes.



ing decrease in the relative occurrence of tipulid larvae in diets that year. This increased use of soldier flies appeared to be relatively transient in that soldier flies only made up 5% and 6% of the diet in the following year (2016) in females and males, respectively. We believe that this reflected better containment of flies at the commercial facility in the second year of operation (G. Olson, Enterra Feed Corporation, personal communication). This pattern was confirmed by data on individual birds. In 2015, every female

( $n = 17$ ) included soldier flies in their diet, and 9/15 (60%) males did so as well. In contrast, in 2016, only 5/19 females and 4/15 males included soldier flies in their diet. There was marked individual variation in the use of soldier flies among individual females (4%–48% of prey items) and males (1%–71% of prey items). However, this variation was continuous and therefore not consistent with the idea of a generalist–specialist dichotomy within species where only some individuals express a specialized diet (Bolnick et al.

2003). The fact that fewer individual birds used soldier flies in 2016 but still had quite high levels of soldier flies in their diet (up to 20%–30%) might represent some level of individual specialization. In previous studies, even when winged insects are available (i.e., represented in the diet), they only made up a minor, but annually variable, component of the diet of European Starlings, e.g., 11% overall, but 1%, 2%, 5% in 3 years and 22% in a 4th year (Rhymer et al. 2012), and <1% (Tinbergen 1981). The sudden use of soldier flies as a more significant component of diet in our study is most likely because the commercial operation provided a localized, concentrated, and easily available source of soldier flies.

Bell (1990) reported that soldier flies (Stratiomyidae) had much lower energy content (12 kJ/g dry mass) compared with tipulid larvae (25.5 kJ/g dry mass). A main goal of our study was therefore to determine if use of novel, potentially nutritionally poor, prey had negative effects on breeding productivity of European Starlings. We found no evidence for this: brood size at fledging and chick quality (mass, tarsus length) were independent of both the number and proportion (%) of soldier flies returned to the nest by females and by both parents. Rather, the number of chicks at fledging, but not chick quality, was positively correlated with the mean number of tipulid larvae returned to the nest per unit time by females, and the mean number of soldier flies returned to the nest per unit time by both sexes. This suggests that breeding productivity is more dependent on the amount of food brought back to the nest rather than the type of prey. In fact, although soldier flies might be lower quality prey, European Starlings using this prey might benefit in other ways: if adult soldier flies are concentrated at the commercial facility, then they can presumably be caught easily, so foraging costs could be lower (e.g., European Starlings were observed picking soldier flies off netting where they were trapped and concentrated; D. Davis, personal communication).

In conclusion, our study suggests that introduction of novel prey to the agricultural landscape used by European Starlings, through a commercial insect farming operation, did not have negative effects on breeding productivity. Nevertheless, given the importance of more traditional pasture habitat and of tipulid larvae for breeding success of European Starlings, broader changes in agriculture clearly have negative effects on European Starling population size. Widespread spraying of grass fields to control dipteran larvae (Campbell and Cooke 1997) and decreases in cattle farming and movement of cattle from pasture to indoor facilities year-round (Heldbjerg et al. 2016) have led to substantial declines in European Starling populations in the U.K. (Robinson et al. 2005) and Europe (European Bird Census Council 2015) since the 1980s. What was once considered a pest species is now listed on the International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species. After a period of increasing population size, the long-term trajectory of European Starling populations across Canada and in British Columbia is also now negative (Environment and Climate Change Canada 2014). Ironically, this is considered a positive change in British Columbia given concerns about this invasive, alien species having negative effects on native species, e.g., through competition with other cavity nesters (Koch et al. 2012; Davidson 2015). European Starlings are a typical agricultural specialist being associated with more traditional, less intensive farming practices (pastures, grassland, etc.; Cabe 1993). Farmland and grassland bird populations have shown marked declines throughout Europe and North America in recent decades due to agricultural intensification and many of the effects of human-induced changes to the agricultural landscape on farmland birds are thought to be mediated by changes in food supply, e.g., the types of insect prey, or decreases in abundance of insect prey, available to breeding birds (Newton 2004; Nocera et al. 2012; Stanton et al. 2018). Nevertheless, direct connections between agricultural change and effects on bird populations due to changes in food availability can be difficult to

demonstrate (Stanton et al. 2018). Commercial insect farming is an increasing component of human-induced change to the agricultural landscape (Dossey et al. 2016; Gahukar 2016) and might provide further opportunities for “natural experiment” that otherwise are difficult to perform. Our study suggests that one specialist species, the European Starling, might be robust to changes in prey type, but clearly more studies of species across the specialist–generalist spectrum would be valuable.

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