Behavioural Processes 108 (2014) 142–150

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Skylarks trade size and energy content in weed seeds to maximize total ingested lipid biomass

Sabrina Gaba[a,*,1], Claire Collas[a,b,1], Thibaut Powolny[c,d], François Bretagnolle[e,f], Vincent Bretagnolle[c,g]

[a] INRA, UMR1347 Agroécologie, 17 rue Sully, F-21065 Dijon Cedex, France
[b] INRA, UMR1213 Herbivores, Centre de Clermont-Ferrand/Theix, 63122 Saint-Genès-Champanelle, France
[c] CEBC, UMR 7372 CNRS – Université de La Rochelle, F-79360 Villiers enBois, France
[d] Office National de la Chasse et de la Faune Sauvage, Carrefour de la Canauderie, 79360 Villiers en bois, France
[e] Université de Bourgogne, UMR6282 Biogéosciences, 6 Boulevard Gabriel, 21000 Dijon, France
[f] UMR 5175 CEFE-CNRS, 1919 Route de Mende, 34293 Montpellier 5, France
[g] LTER « ZA Plaine & Val de Sèvre », CNRS-CEBC, F-79360, Beauvoir sur Niort, France

ARTICLE INFO

Article history:
Received 25 March 2014
Received in revised form 8 September 2014
Accepted 17 October 2014
Available online 28 October 2014

Keywords:
Optimal foraging
Weed
Seed size
Lipid content
Trade-offs
Skylark

ABSTRACT

The trade-off between forage quality and quantity has been particularly studied in herbivore organisms, but much less for seed eating animals, in particular seed-eating birds which constitute the bulk of wintering passerines in European farmlands. The skylark is one of the commonest farmland birds in winter, mainly feeding on seeds. We focus on weed seeds for conservation and management purposes. Weed seeds form the bulk of the diet of skylarks during winter period, and although this is still a matter for discussion, weed seed predation by granivorous has been suggested as an alternative to herbicides used to regulate weed populations in arable crops. Our objectives were to identify whether weed seed traits govern foraging decisions of skylarks, and to characterize key seed traits with respect to size, which is related to searching and handling time, and lipid content, which is essential for migratory birds. We combined a single-offer experiment and a multiple-offer one to test for feeding preferences of the birds by estimating seed intake on weed seed species differing in their seed size and seed lipid content. Our results showed (1) a selective preference for smaller seeds above a threshold of seed size or seed size difference in the pair and, (2) a significant effect of seed lipid biomass suggesting a trade-off between foraging for smaller seeds and selecting seeds rich in lipids. Skylarks foraging decision thus seems to be mainly based on seed size, that is presumably a 'proxy' for weed seed energy content. However, there are clearly many possible combinations of morphological and physiological traits that must play crucial role in the plant–bird interaction such as toxic compound or seed coat.

1. Introduction

Following the optimal foraging theory, predators should maximize the consumption of prey with highest energetic content while minimizing searching and handling times to reduce both predation risk and the cost of prospecting (Krebs, 1980). Hence, consumers should selectively forage for preys according to their size and energy in order to maximize energy intake rate (Sutherland, 1996). Seed-eating birds are among the most pervasive seed predators and numerous factors are involved in seed selection by birds. Some studies report positive associations between the proportion of seeds eaten by birds and the seeds' content of energy (Carrillo et al., 2007; Glück, 1985), lipids (Greig-Smith and Wilson, 1985), protein (Valera et al., 2005), carbohydrates (Kelrick et al., 1986; Ríos et al., 2012a), and water (Carrillo et al., 2007). However, the role of seed size and nutritional quality on foraging intensity and seed selection by birds remains to be established. In particular, whether seed traits govern, or not, the foraging decision by granivorous birds is not known, though this is a prerequisite for any attempt to characterize the relationships between granivorous birds and seeds given that their effects on the dynamics and distribution of plant populations are poorly documented (Marone et al., 2008). On one hand, small seed might be selected due to ease of handling and high encounter probability. On the other, large seeds can also be attractive for granivores due to their high nutritive and energetic values which may

* Corresponding author. Tel.: +33 0 3 80 69 31 87; fax: +33 0 3 80 69 32 62.
E-mail address: sabrina.gaba@dijon.inra.fr (S. Gaba).
[1] These authors contributed equally to this article.

http://dx.doi.org/10.1016/j.beproc.2014.10.004
0376-6357/

compensate for the cost of transport and consumption time (Celis-Diez et al., 2004; Martínez et al., 2006). Seed selection in birds can be heavily conditioned by the seeds' chemical composition combined with the animal's physiological capacities to process nutrients and toxins (e.g. Ríos et al., 2012a). Among the nutritional compounds, lipids are a fundamental dietary component for granivorous birds in winter because they constitute fatty supplies that are mobilized to resist cold temperatures (Blem, 1990; Krams et al., 2010). Moreover, seeds with high oil content may provide a more valuable source of metabolic water for birds (Frank, 1988; Carrillo et al., 2007). Lipids are also essential for migratory birds since they can rapidly mobilize and oxidize them during physical efforts (McCue et al., 2009). However, other constraints may act on seed selection by granivores, such as secondary metabolites (Díaz, 1996; Kelrick et al., 1986; Ríos et al., 2012b). Plants store secondary metabolites in their seeds, some of which can be toxic or reduce digestibility for granivores (Anhalzer et al., 2010; Kerley and Erasmus, 1991; Ramírez and Traveset, 2010). Overall therefore, the traits under selection, as well as the proxy granivorous birds may use to select seeds with regard to energetic inputs, remain a puzzle.

The aim of the present study was to analyze seed preferences of the skylark (*Alauda arvensis*), a farmland specialist passerine bird, in relation to seed trait variation. This species was selected because it is one of the commonest farmland birds in winter, feeding mainly on seeds (Robinson, 2004), and therefore skylarks can be regarded as one of the main seed predators in European farmland landscapes in winter (Boatman et al., 2010; Donald, 2004). Here we use an experimental approach to identify seed trait candidates that may be used by skylarks to select their seed food. Our experiments particularly focused on the possible trade-off between seed oil content and seed size which was quantified by seed mass as they are positively correlated. We selected weed seeds which form the bulk of the diet of skylarks during the critical wintering period (Geiger et al., 2014) and because weed seed predation is suggested as an alternative to herbicides used to regulate weed populations in arable crops (Westerman et al., 2008), although this is still a matter for discussion. Available weed seeds (more than 200 species in typical winter wheat stubbles in, e.g., our study site: Gaba et al., 2010; Meiss et al., 2010) are highly variable with regard to size and lipid content, both traits strongly influencing seed nutritive value. Our experimental design consisted in disentangling the two traits, and choosing weed species in trials so that these two traits were uncorrelated. First, we test whether skylarks seed use is influenced by seed size. We predicted that skylarks will prefer small seeds since they require less energy to be eaten and digested than larger seeds (Thompson et al., 1987). Second, we test whether skylarks seed selection is influenced by seed lipid content. We predicted that skylarks will prefer high lipid content seeds since they would have a higher caloric content than high protein or high carbohydrates seeds (Celis-Diez et al., 2004; Anhalzer et al., 2010). Third, by using multiple-offer tests with pairs of seeds, we test whether skylarks trade mass against lipid content, and which trait, if any, is preferred in the trade-off.

2. Materials and methods

2.1. Capture and housing conditions of skylarks

A total of 105 (55 males and 50 females), wild skylarks were trapped by mist-nets along the French Atlantic coast during post-nuptial nocturnal migration, in five trapping sessions (October–November 2010). During the nights of capture, nets were deployed from 6 pm to 5 am the next morning and, each net was checked every 15 min. Accordingly, birds did not stay more than 15 min (maximum) before they were removed from the net. Birds were maintained from their capture to the next morning in opaque aviaries (60 cm × 50 cm × 50 cm) on the back of our field truck, protected from weather or light. During the capture session, nobody was left in the truck to limit loud noises or disturbance. They were then transported to the laboratory which was between 5 and 8 km. Thus, the transport times were approximately 10 min. The 105 birds were randomly assigned to 10 groups of 10 individuals and acclimatized for 3 months in 4 m × 3 m × 2 m outdoor aviaries, before the start of the experiment. Each cage contained a maximum of five birds. Each aviary contains two different shelters of 2 m^2 each.

Birds were fed ad libitum with a commercial seed mix, grit, oilseed rape and tap water (Powolny et al., 2012). Food and water were respectively dispensed on three synthetic green turfs (height: 1 cm; density: 12 blades/cm^2) and three cup of water (1l each) scattered at different spots in the outdoors aviaries changed daily. Aviaries were placed c. 100 m from any building, in the lab centre, in remote grassland. They were not disturbed since nobody had access to the aviaries. Despite that skylark is a terrestrial species (feeding only on the ground), perches were placed in each aviaries. Only three dead birds were observed (from the 105) during the period in which birds were maintained under captive conditions (from October 2010 to early March 2011, i.e. around the start of spring migration). Therefore the observed mortality rate of c. 3% was much lower than natural winter mortality in this species, which is about 40% (Daunicht, 1998). During the captive period, veterinary checks were performed twice and each bird was weighed weekly. No birds lost weight during the winter, indicating that subordinate birds (if any) did not suffer from competition. After several observations and body mass measures, seven birds showed signs of weakness, i.e. a decrease in their body mass. These birds were isolated from others and each bird was individually treated with Baycox (Bayer Company) against coccidiose by a veterinarian. After a controlling period of two weeks following treatment, birds were weighed and released safe into the wild, under clear weather, in the same place where they were caught. Only birds that did not show any sign of weakness were used for the experiments.

Birds were colour ringed, weighed (±0.1 g), measured (maximum wing chord, tarsus and beak) and the sex of each individual was determined by genetic analysis using blood samples (200 μl) from the brachial vein (Eraud et al., 2006). According to the licence/permit, all birds were returned to the wild after the study period in March 2011 during the pre-nuptial migration. Before being release, skylarks were checked by a veterinarian and the body mass of 90% of the birds was higher after the period in captivity. This work was performed with governmental authorizations from the *Préfecture des Deux-Sèvres* (Niort, France, No. 79-219). All experiments were carried out in compliance with French legal requirements and with the permission of the National Conservation Authority (no. 79349). Bird capture and blood sampling were performed under permit from the National Hunting and Wildlife Agency to TP (No. 2009-014). Animal experiments were in agreement with the guidelines for the treatment and use of animals in behavioural research and teaching as published by the Association of Animal Behaviour (ASAB 2012).

2.2. General experimental design

Experiments started on February 7th and ended on March 9th 2011 at the *Centre d'Etudes Biologiques de Chizé* (West of France). Birds were weighed the evening before each trial and placed into an outdoor aviary without any food until the beginning of the trial the next morning to avoid satiety. We used both multiple- and simple-offer feeding experiments to detect food preferences by skylarks as recommended by Cueto et al. (2006). Trials were