

Vegetation structure and inter-individual distance affect intake rate and foraging efficiency in a granivorous forager, the Eurasian Skylark *Alauda arvensis*

Thibaut Powolny · Cyril Eraud · Jean-Daniel Masson · Vincent Bretagnolle

Received: 23 July 2014/Revised: 7 January 2015/Accepted: 19 January 2015/Published online: 12 February 2015
© Dt. Ornithologen-Gesellschaft e.V. 2015

Abstract Animals gain benefits from group living through increased probability of predator detection, dilution of individual risk and confusion of predators during attack. A further benefit involves larger groups in which individuals may further decrease the amount of time spent being vigilant, while maintaining the probability of predator detection by allocation of this extra time to foraging activities. Living in groups or flocks, however, also incurs costs, e.g., by increasing inter-group competition, with negative impacts on intake rates. Our aim was to investigate the trade-offs between the costs of competition and the benefits of group living in contrasted habitats. For prey species that rely on sight for detecting predators, vegetation structure may influence the perceived predation risk. Hence, we experimentally examined the combined effects of vegetation height and inter-individual distance on foraging time, intake rate and foraging efficiency in a granivorous species, the Eurasian Skylark (*Alauda arvensis*). Our experimental results based on temporally captive birds indicate that time devoted to foraging decreased with increasing inter-individual distance, but was unrelated to cover height. Conversely, increasing both vegetation height and distance with other group members did translate into a foraging disadvantage, i.e. reduced intake rate as well as foraging efficiency. Overall, our results show that both

vegetation structure and inter-individual distances modify patch profitability, and therefore provide another example of how flock dynamics can influence the trade-off between vigilance and foraging.

Keywords Vigilance · Vegetation structure · Inter-individual distance · Competition · Flock size · Aggregative species

Zusammenfassung

Art der Vegetation und Abstände zwischen Einzeltieren beeinflussen Häufigkeit und Effizienz der Nahrungsaufnahme eines Körnerfressers, der Eurasischen Feldlerche (*Alauda arvensis*)

Ein Leben in größeren Gruppen ist für Tiere vorteilhaft, weil dadurch Feinde eher entdeckt werden, das Risiko für jedes einzelne Tier geringer ist und Räuber bei einem Angriff verwirrt werden. Ein weiterer Vorteil liegt darin, dass einerseits jedes Einzeltier weniger Zeit in Wachsamkeit und Aufpassen investieren muss, während andererseits die Wahrscheinlichkeit, Feinde zu entdecken, durch die Gruppe weiterhin hoch bleibt. Dadurch gewinnt jedes einzelne Tier zusätzliche Zeit, die für die Nahrungsaufnahme genutzt werden kann. Das Leben in Gruppen, oder Schwärmen, hat jedoch auch seine Kosten: eine erhöhte Konkurrenz zwischen den einzelnen Tieren innerhalb der Gruppe mit entsprechend negativen Auswirkungen auf die Nahrungsaufnahme. Ziel unserer Studie war, in unterschiedlichen Lebensräumen die Vorteile des Gruppenlebens gegen die Nachteile der intensiveren Konkurrenzsituation abzuwägen. Bei Tieren von Beutearten, die davon abhängen, Räuber so rasch wie möglich zu entdecken, beeinflusst die Struktur der Vegetation vermutlich das empfundene Risiko,

Communicated by F. Bairlein.

T. Powolny (✉) · C. Eraud
Office National de la Chasse et de la Faune Sauvage (ONCFS),
Carrefour de la Canauderie, 79360 Villiers en Bois, France
e-mail: thibaut.powolny@yahoo.fr

T. Powolny · J.-D. Masson · V. Bretagnolle
Centre d'Études Biologiques de Chizé, Centre National de le
Recherche Scientifique (CNRS), 79360 Villiers en Bois, France

erbeutet zu werden. Deshalb überprüften wir für eine körnerfressende Art, die Eurasische Feldlerche (*Alauda arvensis*), experimentell den kombinierten Effekt von Vegetationshöhe und Abständen zwischen den Einzeltieren auf die Dauer, Häufigkeit und Effizienz der Nahrungsaufnahme. Die Ergebnisse unserer Experimente mit zeitweise gekäfigten Vögeln zeigen, dass die für die Nahrungsaufnahme verwendete Zeit mit wachsenden Abständen zwischen den Einzeltieren abnahm, es aber keinen Zusammenhang mit der Vegetationshöhe gab. Wurde jedoch beides, die Vegetationshöhe und die Abstände zu anderen Gruppenmitgliedern, erhöht, ergab sich daraus ein Nachteil für die Ernährung: eine Verminderung sowohl der Häufigkeit als auch der Effizienz der Nahrungsaufnahme. Unsere Ergebnisse zeigen, dass beides, die Vegetationsstruktur und die Abstände zwischen Einzeltieren, Auswirkungen auf den Nahrungs-Ertrag haben können und liefern so ein weiteres Beispiel dafür, wie die Schwarmdynamik den trade-off, das Ausbalancieren der Vor- und Nachteile, von Nahrungsaufnahme und Wachsamkeit beeinflussen kann.

Introduction

Many animal species exhibit cohesive aggregation, with familiar examples being mammalian herding, insect swarming, or bird flocking (Schellinck and White 2011). To account for this striking behaviour, a commonly proposed argument relies on expected benefits of aggregating with conspecifics in terms of decrease of individual predation risk (Krause and Ruxton 2002), either by dilution of predation risk (Foster and Treherne 1981) or by collective detection (Hilton et al. 1999). However, there are also costs to aggregation, since living close to neighbours may increase competition for food among group members (Wrangham 1980). Such costs arise either through contest competition for food, which may indeed lead to decreased foraging intake rate (Beauchamp 2009) because individuals devote time to agonistic behaviours, or alternatively scramble competition (Teichroeb and Sicotte 2012), which does not involve direct aggression, but pre-emption over resources by another individual (Janson 1988). Scramble competition is likely when individuals increase their foraging effort (by moving further, feeding faster, etc.) if close to other foragers as compared to when they are solitary or far from conspecifics (Chapman and Chapman 2000).

Bird species that aggregate have long been studied in regards to the trade-off between the benefits in terms of predation versus the costs in terms of competition for food (Rolando et al. 2001). Many such studies have shown that the trade-off is actually impacted by several

factors including food density (Beauchamp 1998), habitat structure and its influence on the perceived predation risk (Butler et al. 2005a; Verdolin 2006), the position in the flock (Beauchamp 2013) or the group size (Fernandez-Juricic et al. 2007). Neighbour distance is thought as a determinant factor governing the foraging/vigilance trade-off (Cowlshaw 1998; Treves 1998; Steenbeck et al. 1999; Rolando et al. 2001), and it has often been suggested that the proximity of conspecifics might be the perceptible unit of safety in group-living individuals (Lima 1995; Roberts 1996; Treves 2000). The cost of grouping may thus be mediated by adjusting distances among group members (Aureli et al. 2008). Although the effects of the inter-individual distance in groups have been previously investigated (e.g. Valone 1993; Templeton and Giraldeau 1995; Fernandez-Juricic et al. 2004), their combined effects with vegetation structure remain poorly known. For species that rely on sight for detecting predators, vegetation structure may influence the perceived predation risk (Lima and Dill 1990), and is therefore likely to affect foraging habitat selection (Butler et al. 2005b) as well as anti-predator strategies. For some species, vegetation is perceived as being largely protective, reducing the risk of predator detection (Ekman 1987; Högstad 1988). In contrast, some species perceive vegetation as obstructive, reducing the likelihood of early predator detection, and patches with increased vegetation structure are likely to have a higher associated predation risk (Metcalf 1984).

In this study, we explore the behavioural consequences of neighbours distance and vegetation structure on foraging activities in regard to aggregation using the Eurasian Skylark (*Alauda arvensis*) (hereafter Skylark) as a study model. Indeed, while the Skylark is known to be mostly territorial and to feed mainly on insects during the spring and summer (Cramp 1988), the species changes its behaviour during migration and wintering periods, when birds forage essentially on plant material and form large flocks (Cramp 1988). While most studies dealing with the winter ecology of this species have so far focused on habitat use, diet or numerical response to food availability (Wilson et al. 1997; Gillings and Fuller 2001; Geiger et al. 2014), we used an experimental approach in order to manipulate vegetation height and inter-individual distances under captive conditions. Recently, we explored the trade-off between foraging and vigilance in this species foraging on artificially created stubble substrates in aviary conditions (Powolny et al. 2014). As predicted, Skylarks increased their vigilance levels when foraging in obstructed patches. These results suggest that foraging in patches with reduced visibility may impose the dual costs of reduced foraging efficiency and increased predation risk.

Theory predicts a differential response in terms of foraging under different perceived predation risk levels for aggregative species (Krause and Ruxton 2002), but several additional confounding factors may further balance this relationship, such as scrounging competition (Beauchamp 2009). If so, we hypothesise that Skylarks might differentially behave in response to the perceived predation risk according to inter-individual distance between group members. Especially, if scramble competition is negligible in this aggregative species, we predict that a negative effect of vegetation height on foraging may be attenuated when Skylarks forage close to other group members.

Methods

Captive conditions and subjects

The study was conducted at the Centre d'Etudes Biologiques de Chizé (western France) from 8 February to 3 March 2012. We caught Skylarks along the Atlantic flyway during the post-nuptial migration, between October and November 2011. Upon capture, the birds were colour-ringed, measured (tarsus and maximum wing chords) and weighed (precision: ± 0.1 g; males: 41.1 ± 0.2 g; females: 36.7 ± 0.22 g). Blood samples were taken, and their sex was obtained from molecular analysis (see Eraud et al. 2006 for details). Thereafter, birds were randomly assigned to groups of 10–12 individuals and acclimatized for 2 months in $4 \times 3 \times 2$ m ($l \times w \times h$) outdoor aviaries. The experimental location was 50 m away from the closest building, which received very low pedestrian traffic, thus minimizing noise and disturbance. Birds were fed ad libitum with a commercial seed mixture, grit, fresh oilseed rape and tap water. Food was dispensed on a 2-m^2 synthetic green turf (height: 1 cm; density: 12 blades/cm²) to acustom individuals to the experimental set-up (see below). Skylarks responded well to this situation and quickly started foraging in the same general way as when free. Previous study showed that the presence of enclosures did not noticeably perturb their daily activities (Powolny et al. 2012). All birds were released into the wild in early March, during the pre-nuptial migration.

General experimental procedures

The night before each trial, all focal birds were weighed and deprived from food (for a total time of 12–16 h) until the next morning. Trials were only performed from 0800 to 1200 hours in order to avoid long fasting periods. We did not conduct experiments on rainy or excessively windy days, as these extreme weather conditions would likely affect visibility and foraging behaviour. All trials were

carried out in a separate outdoor aviary, showing identical proportions and layout to the housing aviaries.

We experimentally exposed birds to contrasting vegetation height (2 levels) and conspecific distance (3 levels). Each bird was exposed to all of the 6 treatment combinations in a random order during the total duration of the experiment (c. 1 month). The experimental arena consisted of a $50 \times 50 \times 40$ cm wire cage (mesh size 1×1 cm) enabling visual contact amongst birds. This cubic cage was placed over an artificial green turf substrate surrounded or not by stubble. To mimic natural stubble habitat, we attached cereal straw to a brown polystyrene board. The straw was arranged in rows 12 cm apart at a density of 110 straws/m, which was equivalent to the density measured in natural stubble fields around our laboratory ($n = 12$; mean \pm SE; 12.4 ± 2.21 cm; 110 ± 7 straws/m). To investigate the influence of vegetation height on foraging activities, we used two different stubble heights: 0 cm (no stubble) and 15 cm in height (comparable to the height measured in 20 randomly selected patches in 5 stubble fields (mean \pm SE = 15.2 ± 1.87 cm; range 9.8–17.3) in the same season. To investigate the influence of neighbours' distances, four similar cubic cages were placed at three levels of separation (0, 1 and 3 m). This led to inter-Skylark distances within the range observed in natural Skylark foraging flocks (Powolny et al., unpublished data). The enclosures were arranged in a triangle surrounding the focal bird, with one non-focal bird in each summit (Fig. 1). As food source, we used millet seeds (*Panicum miliaceum*) owing to their homogeneity in both colour (white) and size (mass = 0.007 ± 0.0003 g; $n = 300$ seeds). Only the focal birds were exposed to one unique seed density ($1,000$ seeds m^{-2}) randomly scattered on the artificial green turf substrate. This seed density corresponds to the mean seed density founded in the field during from December to March in stubble ($n = 41$; mean \pm SE; $1,400 \pm 340$ seeds m^{-2} , Powolny 2012).

Totals of 10 male and 10 female birds served as focal individuals. All combinations of the two levels of vegetation height and the three neighbour distances were tested. Each focal bird experienced one replicate for each combination of separation and vegetation height. Hence, we conducted 120 trials. The remaining non-focal birds were randomly assigned to complete the four-bird group in the trials and were individually kept in identical wire mesh cages. To avoid synchrony in behaviour (see Fernandez-Juricic and Kacelnik 2004), non-focal birds were not provided with food during tests. There were between six and eight trials per day, but neither the focal nor the non-focal birds experienced more than one trial in any one day. Group composition thus varied from test to test to avoid systematic association between partner birds and experimental treatments. Group sex-ratio was always equal to one, with two females and two males,

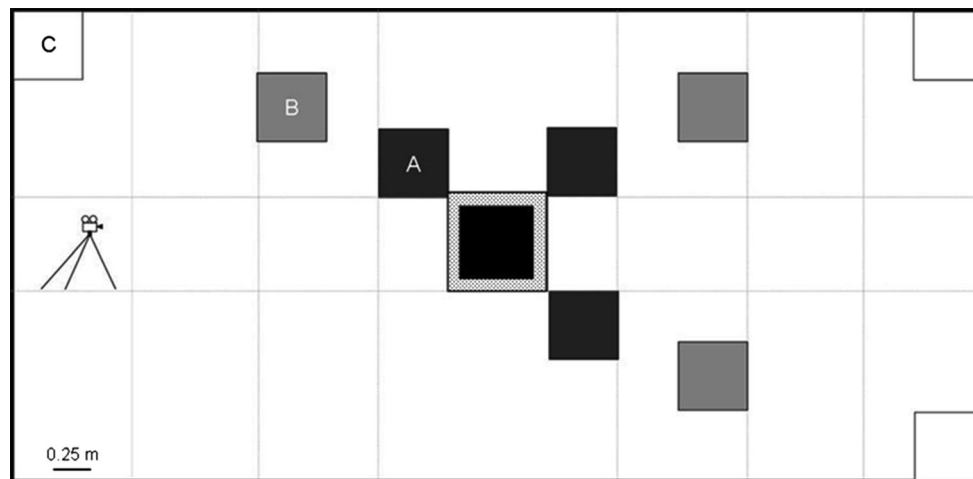


Fig. 1 Experimental set-up showing the location of the four bottomless enclosures placed at different distances ($d = 0, 1$ and 3 m), the relative position of the camera recording the behaviour of the focal Eurasian Skylark *Alauda arvensis*, and the placement of the

partitions. Complete *black square* represent the position of the focal bird, *a* the position of the conspecific with a inter-individual distance of 0 m, *b* the position at 1 m and *c* the position of non-focal birds at 3 m. The *dotted area* represents the area where stubbles were placed

independently of the focal bird sex. Ten minutes before each trial, birds were transported in soft bags and were placed in their respective cages so that they became accustomed to the device. The observer was hidden and positioned approximately 10 m from the focal bird enclosure. The behaviour of the focal bird was recorded on a video camera placed 1 m above the ground and about 2 m from the focal bird. Based on previous experience with a similar set-up (Powolny et al. 2012), we used 5 -min trials, which started when the subjects began pecking. Trial duration was short enough to keep the birds foraging actively (no satiation effects were observed).

Data collection

The behaviour of focal birds was analysed from videotapes using an event-recording program (EthoLog 2.2; Ottoni 1996). All videos ($n = 120$) were analysed at $1\times$ reading speed after testing on a subset of trials that this speed provided correlated results to those obtained by analyzing the videos frame by frame (e.g. for foraging time, Pearson correlation coefficient: $r = 0.781$; $p < 0.01$, $n = 90$ trials). Using video recording, the posture of birds was analysed for each trial. Following Whittingham and Markland (2002) and previous work (Powolny et al. 2012), a bird was considered to be vigilant when its head was above the horizontal line made by its body, and not orientated towards the ground. Conversely, a bird was considered as foraging when its head was below the horizontal line and when it actively scanned the ground or pecked. Although head-down posture is associated with foraging behaviour, this position may still allow vigilance (Fernandez-Juricic

et al. 2004). Thus, we added a 5 -cm-high opaque band around the bottom of the cage of the focal bird, which completely precluded any visual contact between a foraging focal individual and its neighbours. At the end of each trial, seeds remaining on the green turf were counted by hand by the same person, without information about trial conditions (inter-individual distance or vegetation height). The corresponding values were used to calculate food intake rate (expressed as the number of seeds consumed during the 5 -min trial). A proxy of the foraging efficiency was expressed as the residuals of the linear regression ($n = 120$; $r^2 = 0.29$) between the number of seed consumed and the time devoted to actively searching for food during the 5 -min trial (Goulson et al. 2002). J.D.M. performed all video analyses after extensive self-training in analysing pilot videotapes.

Statistical analyses

We used general linear mixed models (GLMMs) to investigate the effects of vegetation height and inter-individual distances between focal and neighbour birds, on foraging time, intake rate and foraging efficiency. Because focal individuals were tested for all treatment combinations, models were fitted with bird identity as a random factor, nested within sex. Analyses were separately performed for each dependent variable and followed a backward selection procedure starting from a departure model that included all factors and all their two-way interactions and a set of continuous covariates designed to control for the conditions in which the tests were conducted (see Table 1 for details about covariates). Starting by continuous covariates, non-significant terms at $p = 0.05$ were

sequentially removed. Wherever an interaction term was retained in a model, the two corresponding factors were also left as main effects. Post hoc comparisons were performed using Student’s *t* tests. Foraging times were log-transformed while both intake rate and foraging efficiency were square-root transformed to ensure normality and homoscedasticity assumptions. All analyses were performed using SPSS software. Means are expressed ±SE.

Results

We found no evidence that the foraging behaviour of birds varied according to date, fasting duration or the ambient temperature experienced the night that preceded the trials since these covariates were systematically removed during model selection (Table 2).

Our experiment revealed that foraging time increased with increasing vegetation height ($F_{1,96} = 6.37$; $p = 0.012$).

However, while the interaction term between sex and vegetation height was non-significant ($F_{1,96} = 3.44$; $p = 0.066$), the effect of vegetation height on foraging time seemed to be positive for females (Fig. 2), for which foraging time increased significantly ($t = -1.83$; $p = 0.036$) from 11.78 ± 1.59 s without vegetation to 18.08 ± 2.45 s with a stubble height of 15 cm. Conversely, males did not show variation in foraging time (0 cm: 15.24 ± 0.92 s; 15 cm: 15.02 ± 0.90 s; $t = 1.91$; $p = 0.178$). Without vegetation, males allocated more time to foraging than females ($t = 1.85$; $p = 0.035$). Furthermore, foraging time was not affected by neighbour distance (Table 2). Finally, the time devoted to foraging was impacted by the body condition (individuals with a higher body condition spent less time foraging, $F_{1,96} = 11.26$; $p < 0.001$) and a two-way interaction between sex and body condition ($F_{1,96} = 4.36$; $p = 0.039$).

Despite the increase in foraging time, intake rate decreased with increasing vegetation height ($F_{1,98} = 7.04$; $p = 0.008$; Table 2; Fig. 2), from 28.03 ± 1.13 seeds/trial

Table 1 Explanatory variables entered into models for the foraging time and intake rate studies in captive Eurasian Skylarks *Alauda arvensis*

Variables	Factor/covariate	Description
Inter-individual distance	Factor	0, 1 or 3 (m)
Vegetation height	Factor	0 or 15 (cm)
Sex	Factor	Male or female
Body condition	Continuous covariate	Residuals from linear regression (body mass ~ wing length)
Date	Continuous covariate	In Julian date (1 for 1st January)
Minimum ambient temperature	Continuous covariate	Minimum ambient temperature the night before being tested
Food deprivation	Continuous covariate	In minutes
Foraging efficiency		Residuals from linear regression (Intake ~ foraging time)
Foraging time		Time devoted to actively searching for food (based on head and bill position); expressed in seconds
Intake		Number of seeds consumed per test

Intake rate was calculated after trials as the number of seed proposed minus the total remaining seeds

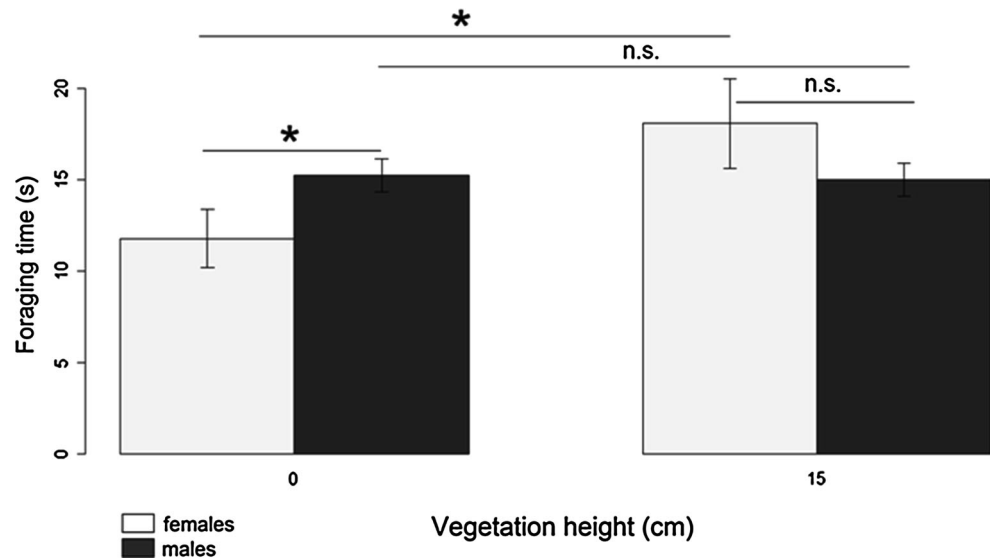
Table 2 Fixed effects explaining variation in time allocated to foraging, intake rate and foraging efficiency in captive Skylarks

Variables	Fixed effect	Df/DfDen	F values	Estimates	P	R ²
Intake	Sex	$F_{1,18}$	4.48	Male: 8.42	0.049*	0.52
	Inter-individual distance	$F_{1,98}$	14.65	1: -6.9	<0.001***	
				3: -10.08		
Foraging time	Vegetation height	$F_{1,98}$	7.04	15: -5.32	0.008**	0.59
	Sex	$F_{1,18}$	1.78	Male: 0.19	0.181	
	Body condition	$F_{1,96}$	11.26	-0.10	<0.001***	
	Vegetation height	$F_{1,96}$	6.37	15: 0.19	0.012*	
	Sex × body condition	$F_{1,96}$	4.36		0.039*	
	Sex × vegetation height	$F_{1,96}$	3.44		0.066	
Foraging efficiency	Sex	$F_{1,18}$	9.45	Male: 9.22	0.007**	0.48
	Inter-individual distance	$F_{1,98}$	18.16	1: -5.14	<0.001***	
				3: -9.83		
	Vegetation height	$F_{1,98}$	12.13	15: -6.56	<0.001***	

A minimal model was backward-selected using a linear mixed effect model with individual identity as a random effect

Symbol of significance: *** $P = 0$; **0.001; *0.01; 0.05

Fig. 2 Effects of vegetation height on average foraging time (s) in captive Skylarks. *Black histograms* represent males and *white histograms* represent females. The represented effects were controlled for co-variables in the values plotted in the graphs. *Vertical bars* standard errors



on average without vegetation, to 22.72 ± 1.13 seeds/trial with 15 cm vegetation height. In addition, there was a negative effect of inter-individual distance on intake rate ($F_{1,98} = 14.65$; $p < 0.001$), with no interaction between vegetation height and neighbour distance. Skylarks foraging in a patch closer to neighbours consumed on average 31.05 ± 1.29 seeds/trial, while those foraging in the farthest patch from conspecifics (i.e., 3 m) had a reduced intake rate (20.98 ± 1.29 seeds/trial). Intermediate values were recorded at medium distance (i.e., 1 m: 24.10 ± 1.29). Skylarks significantly reduced their intake rate at 1 m in comparison to a distance of 0 m (31.05 ± 1.29 ; $t = 2.18$; $p = 0.032$), and between a distance of 3 m and 0 m ($t = 3.28$; $p = 0.002$).

We observed a significant sex effect on intake rate ($F_{1,18} = 4.48$; $p = 0.049$), with males intake rate being higher than that of females (respectively, 29.58 ± 1.04 vs. 21.17 ± 1.05 seeds/trial; $t = 3.29$; $p = 0.001$; Fig. 3). Foraging efficiency was also influenced by sex ($F_{1,18} = 9.45$; $p = 0.007$), inter-individual distance ($F_{1,97} = 18.16$; $p < 0.001$) and vegetation height ($F_{1,97} = 12.13$; $p < 0.001$; Fig. 4; Table 2). Males showed a higher foraging efficiency than females ($t = 4.05$; $p < 0.001$). Foraging efficiency was also higher when the degree of visual obstruction and the distance with the conspecifics were low (Fig. 4; Table 2).

Discussion

Using an experimental setting, our results suggest that the behaviour of foraging Skylarks is influenced by both vegetation height and distance from conspecifics. Birds showed lower intake rates when the vegetation height was

higher and the number of consumed seeds decreased when individuals were farthest. Similarly, the foraging efficiency—measured as the number of seed consumed per second under foraging posture—decreased significantly with increasing vegetation height and distance from conspecifics.

Compared with species in which individuals forage alone, group members can benefit or suffer from aggregation either by scrounging and interference competition (Lima et al. 1999; Sansom et al. 2008), by using information about food location or food quality (public information; Valone and Templeton 2002), or by benefiting from collective detection or mortality dilution per predator attack (Foster and Treherne 1981). Visual obstruction and inter-individual distance should thus play an important role in such context. Within a group, individuals may either receive information derived from external cues, such as the presence of potential predators, or from conspecifics. However, in both cases collecting information will depend on the capacity of individuals to scan their environment and on the proximity between the other members of the group. While it is commonly assumed that individuals gain information about the presence and position of other group members through visual scanning (Fernandez-Juricic et al. 2004), many aggregative animals also give frequent contact calls while foraging (Palombit et al. 1999).

When Skylarks foraged far from conspecifics, foraging activities were disrupted. Similar results (i.e. a lower rate of foraging activity) have been reported for the same species when individuals foraged alone or in small group-size (Powolny et al. 2012) and could be interpreted as responses to higher perceived predation risk. Detection and production of shared information about the predator should decline with distance from the predator. Such distance

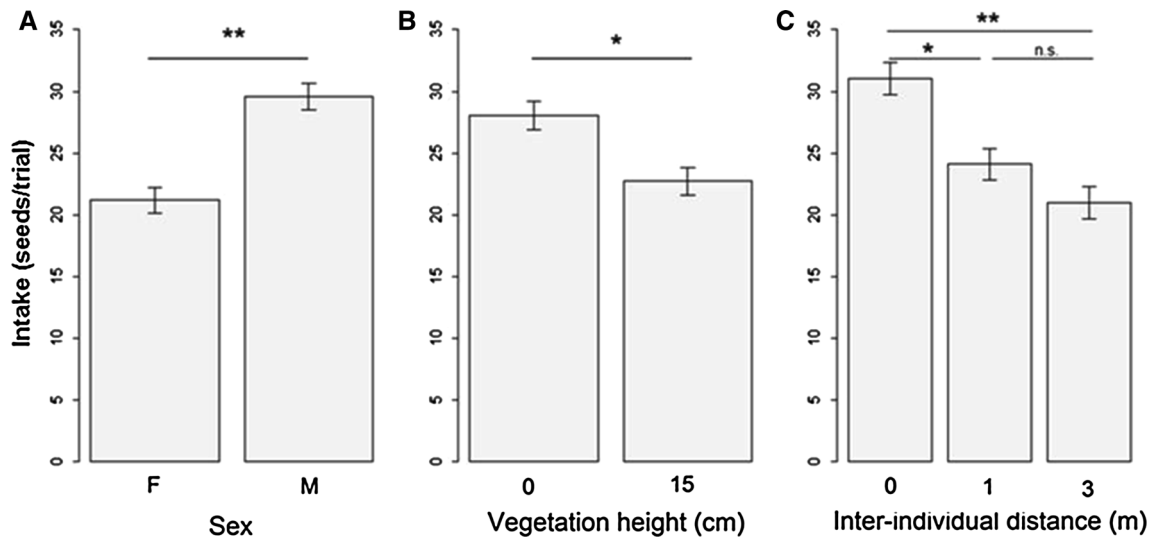


Fig. 3 Effect of sex (a), vegetation height (b) and inter-individual distance (c) on seed intake in captive Skylarks. The represented effects were controlled for co-variables in the values plotted in the

graphs (estimated marginal means). Seed intake data was sqrt-transformed to normalize their distribution. Vertical bars standard errors

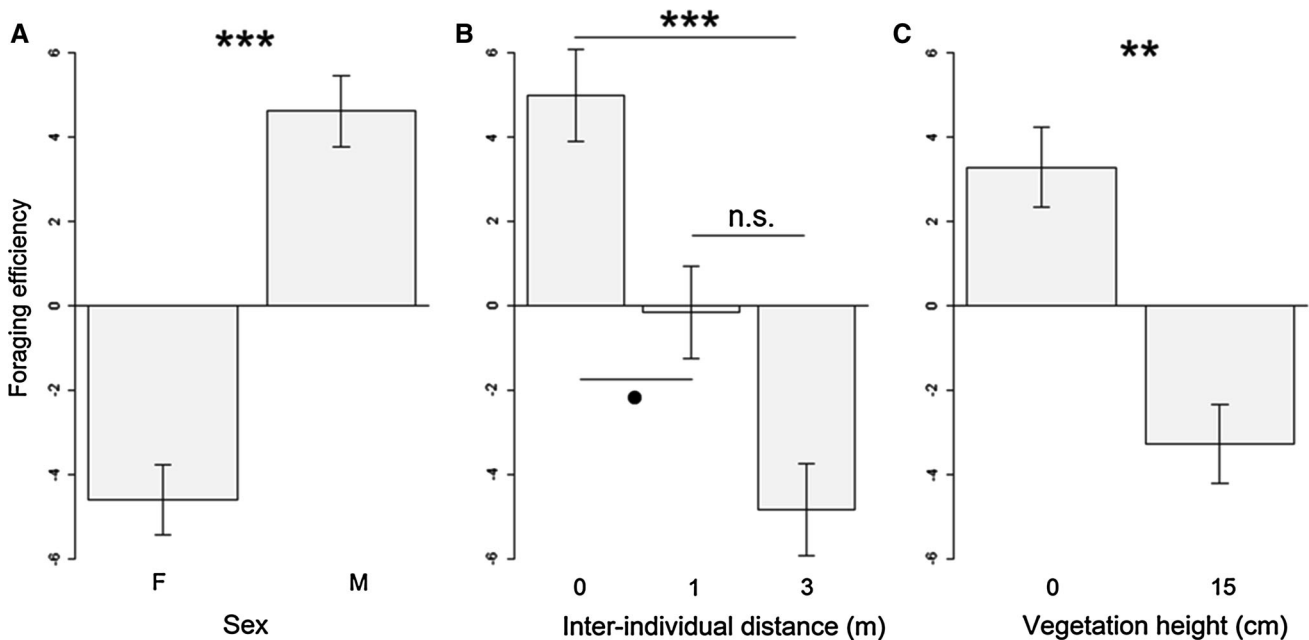


Fig. 4 Effects of sex (a), inter-individual distance (b) and vegetation height (c) on foraging efficiency in captive Skylarks. The foraging efficiency was expressed as the residuals of the linear regression ($n = 120$; $r^2 = 0.29$) between the number of seed consumed and the time devoted to actively searching for food during the 5-min trial. The

represented effects were controlled for co-variables in the values plotted in the graphs (estimated marginal means). Foraging efficiency data was log-transformed to normalize their distribution. Vertical bars standard errors

dependence has been experimentally demonstrated in birds (Lima and Bednekoff 1999; Tisdale and Fernandez-Juricic 2009) and is expected to be more extreme in smaller birds such as Skylarks because visual acuity declines with body size (Kiltie 2000). Skylarks are thus likely to keep sight of group members within a short distance, and they probably monitor group members visually and adjust their

movements to keep cohesiveness with other group members in the field. While increased perceived predation risk due to patch characteristics had strong effects on foraging, variability exists among studies considering vegetation height as an indication of predation risk (Verdolin 2006). For many species, foraging in protective cover considerably reduces perceived risk of predation (Caraco et al.

1980; Rohner and Krebs 1996). Thus, low-risk habitats are defined by the presence of cover, while the absence of vegetation is indicative of higher predation risk. However, and especially for species found in open habitats such as farmland, the lack of cover may be considered as the low predation risk habitat (see Brown et al. 1997 on Crested Lark *Galerida cristata*; Butler et al. 2005a on chaffinches *Fringilla coelebs*). Perhaps, the best illustration of the differences in cover perception between species comes from analysing variation in hedgerow use. Robinson and Sutherland (1999) found that wintering Skylarks in the UK depleted food resources in the middle of fields first, and only moved closer to hedgerows once food became less abundant in field centres. Conversely, the Yellowhammers (*Emberiza citrinella*), another typical farmland bird, were far more likely to forage close to hedgerows. These differences between species attending similar habitats are most likely to be explained by their different strategies in predator avoidance. Yellowhammers seek cover to protect them from attack and so select foraging areas close to the hedges. Conversely, Skylarks employ very different strategy by either taking to the air and attempting to out-fly their predators or by crouching (Cresswell 1994; Butler et al. 2005b). However, contrasting results are available regarding Skylark habitat choice and vegetation height. According to studies in the UK and the Netherlands, Skylarks seem prefer some vegetation cover over bare soil and longer stubbles over shorter stubbles (Donald et al. 2001; Butler et al. 2005b; Whittingham et al. 2006; Geiger et al. 2014). The differences observed between these field studies and our experimental work may be explained by the seed abundance or diversity. In that case, the fields with higher vegetation heights may potentially contain a more important abundance or diversity of seed and would be privileged independently of vegetation height when foraging benefits are higher (Butler et al. 2005a).

Competition is also affected by group members distance, with animals in more compact flocks often being subject to higher levels of competition (Clark and Mangel 1986). When we investigated the change in foraging activities in Skylarks, we showed an effect of inter-individual distance with higher intake rate at short distances. This result suggests no interference competition in our experimental set-up. However, the fact that conspecifics in our experimental design were not fed during tests will likely have affected their scanning behaviour, allowing the focal birds to spend more time foraging. Moreover, because conspecifics were not foraging at all may have reduced the chances of the focal birds of perceiving cues relative to food competition. Along similar lines, the seed density used in our experiment (i.e., 1,000 seeds m^{-2}) did not translate into a limiting factor for the focal bird. In fact, birds consumed only about 22–31 seeds per trail,

suggesting that it seems unlikely that competition for food was a driving factor in our experiment. Further studies are required to explore the effects of contest competition and food density. In our design, we used a seed density corresponding to an average value found throughout winter (i.e., 1,000 seeds/ m^2) in such farmland landscapes (Powolny 2012). According to Moorcroft et al. (2002) and Powolny (2012), strong food depletion is likely to occur within agro-ecosystems during winter and high variation can be found in seed densities. In accordance, later in winter, lower food density is present and may impact the level of inter-individual competition (Cresswell 1998). Moreover, several laboratory studies have provided evidence that group foraging may increase the rate at which food patches are located in the environment, thereby reducing the per capita time spent searching for food (Krebs et al. 1972).

In addition to vegetation height and inter-individual distance, the body condition and the sex of birds influenced the foraging/vigilance trade-off. Individuals with highest body condition were also those with the shortest foraging times, suggesting lower energetic needs and an optimization of immediate survival by avoiding predation (Pelletier and Festa-Bianchet 2004), whereas individuals in lower condition favour consumption and stockpiling (Zimmer et al. 2011).

Skylark behaviours indicate that they are trading-off foraging considerations against the perceived risk of predation. Highly aggregative species, such as Skylarks in winter, are better able to cope with high levels of predation when individuals forage close to each other, and thus may be able to gain higher intake rates as well as anti-predator benefits. However, especially in late winter when the seed resource becomes scarce, higher competitive levels and social dominance may alter the foraging/predation trade-off. Dominant birds may have greater access to food resources, and a relationship between rank and access to feeding sites have been suggested to result in a better survival for high-ranking animals (Desrochers et al. 1988). Thus, further experiments, including the study of food density variations and hierarchical dominance, are needed to better understand this trade-off in the context of group living.

Acknowledgments We thank V. Rocheteau for assistance during fieldwork, N. Guillon, and X. Duchemin for caring for the birds while in captivity and two anonymous reviewers whose comments greatly improved the manuscript. This work was performed with governmental authorizations from the Préfecture des Deux-Sèvres (Niort, France, No. 10.79-219). All experiments were carried out in compliance with French legal requirements. The protocol was approved by the Committee on the Ethics of Animal Experiments of the National Conservation Authority (Permit No. 79349). Bird captures were performed under permit from the National Hunting and Wildlife Agency to TP (No. 2009-014). T.P. was funded by a PhD grant from ONCFS.

References

- Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier KB, Van Schaik CP (2008) Fission-fusion dynamics: new research frameworks. *Curr Anthropol* 49:627–654
- Beauchamp G (1998) The effect of group size on mean food intake rate in birds. *Biol Rev* 73:449–472
- Beauchamp G (2009) How does food density influence vigilance in birds and mammals? *Anim Behav* 78:223–231
- Beauchamp G (2013) Social foragers adopt a riskier foraging mode in the center of their groups. *Biol Lett* 9:05–28. <http://dx.doi.org/10.1098/rsbl.2013.0528>
- Brown JS, Kotler BP, Mitchell WA (1997) Competition between birds and mammals: a comparison of giving-up densities between crested larks and gerbils. *Evol Ecol* 11:757–771
- Butler SJ, Whittingham MJ, Quinn JL, Cresswell W (2005a) Quantifying the interaction between food density and habitat structure in determining patch selection. *Anim Behav* 69:337–343
- Butler SJ, Bradbury RB, Whittingham MJ (2005b) Stubble height affects the use of stubble fields by farmland birds. *J App Ecol* 42:469–476
- Caraco T, Martindale S, Pulliam HR (1980) Avian time budgets and distance to cover. *Auk* 97:872–875
- Chapman CA, Chapman LJ (2000) Determinants of group size in social primates: the importance of travel costs. In: Boinski S, Garber P (eds) *On the move: how and why animals travel in groups*. University of Chicago Press, Chicago, pp 24–42
- Clark CW, Mangel M (1986) The evolutionary advantages of group foraging. *Theor Pop Biol* 30:45–75
- Cowlshaw G (1998) The role of vigilance in the survival and reproductive strategies of desert baboons. *Behaviour* 135:431–452
- Cramp S (1988) *The birds of the Western Palearctic*, vol 5. Oxford University Press, Oxford
- Cresswell W (1994) Song as a pursuit-deterrent signal, and its occurrence relative to other anti-predator behaviours of sky-lark (*Alauda arvensis*) on attack by merlins (*Falco columbarius*). *Behav Ecol Sociobiol* 34:217–223
- Cresswell W (1998) Variation in the strength of interference competition with resource density in blackbirds, *Turdus merula*. *Oikos* 81:152–160
- Desrochers A, Hannon SJ, Nordin KE (1988) Winter survival and territory acquisition in a northern population of Black-capped Chickadees. *Auk* 105:727–736
- Donald PF, Buckingham DL, Moorcroft D, Muirhead LB, Evans AD, Kirby WB (2001) Habitat use and diet of skylarks *Alauda arvensis* wintering on lowland farmland in southern Britain. *J App Ecol* 38:536–547
- Ekman J (1987) Exposure and time use in willow tit flocks: the cost of subordination. *Anim Behav* 35:445–452
- Eraud C, Lallemand J, Lormee H (2006) Sex-ratio of skylark *Alauda arvensis* in relation to timing of breeding: capsule earlier broods tend to be more male biased than later broods. *Bird Study* 53:319–322
- Fernandez-Juricic E, Kacelnik A (2004) Information transfer and gain in flocks: the effects of quality and quantity of social information at different neighbour distances. *Behav Ecol Sociobiol* 55:502–511
- Fernandez-Juricic E, Erichsen JT, Kacelnik A (2004) Visual perception and social foraging in birds. *Trends Ecol Evol* 19:25–31
- Fernandez-Juricic E, Beauchamp G, Bastain B (2007) Group-size and distance to neighbours effects on feeding and vigilance in brown-headed cowbirds. *Anim Behav* 73:771–778
- Foster WA, Treherne JE (1981) Evidence for the dilution effect and the selfish herd from fish predation on a marine insect. *Nature* 293:466–467
- Geiger F, Hegemann A, Gleichman M, Flinks H, de Snoo GR, Prinz S, Tieleman BI, Berendse F (2014) Habitat use and diet of skylarks (*Alauda arvensis*) wintering in an intensive agricultural landscape of the Netherlands. *J Ornithol* 155:507–518
- Gillings S, Fuller R (2001) Habitat selection by skylarks *Alauda arvensis* wintering in Britain in 1997/98. *Bird Study* 48:293–307
- Goulson D, Peat J, Stout J, Tuckers J, Darvill B, Derwent L, Hughes WHO (2002) Can alloethism in workers of the bumblebee, *Bombus terrestris*, be explained in terms of foraging efficiency? *Anim Behav* 64:123–130
- Hilton GM, Cresswell W, Ruxton GD (1999) Intraflock variation in the speed of escape—flight response on attack by an avian predator. *Behav Ecol* 10:391–395
- Högstad O (1988) Social rank and antipredator behaviour of willow tits *Parus montanus* in winter flocks. *Ibis* 130:45–56
- Janson CH (1988) Intra-specific food competition and primate social structure: a synthesis. *Behaviour* 105:1–17
- Kiltie RA (2000) Scaling of visual acuity with body size in mammals and birds. *Funct Ecol* 14:226–234
- Krause J, Ruxton GD (2002) *Living in groups*. Oxford University Press, Oxford
- Krebs J, MacRoberts M, Cullen J (1972) Flocking and feeding in the great tit *Parus major*: an experimental study. *Ibis* 114:507–530
- Lima SL (1995) Back to the basics of anti-predatory vigilance: the group-size effect. *Anim Behav* 49:11–20
- Lima SL, Bednekoff PA (1999) Back to the basics of antipredatory vigilance: can non-vigilant animals detect attack? *Anim Behav* 58:537–543
- Lima L, Dill LM (1990) Behavioral decisions made under the risk of predation. A review and prospectus. *Can J Zool* 68:619–640
- Lima SL, Zollner PA, Bednekoff PA (1999) Predation, scramble competition, and the vigilance group size effect in dark-eyed juncos (*Junco hyemalis*). *Behav Ecol Sociobiol* 46:110–116
- Metcalfe NB (1984) The effects of habitat on the vigilance of shorebirds: is visibility important? *Anim Behav* 32:981–985
- Moorcroft D, Whittingham MJ, Bradbury RB, Wilson JD (2002) The selection of stubble fields by wintering granivorous birds reflects vegetation cover and food abundance. *J App Ecol* 39:535–547
- Otoni EB (1996) *Etholog 1.0: ethological transcription tool for Windows*. Behavior Research Methods, Instruments and Computers 28:472–473
- Palombit RA, Cheney DL, Seyfarth RM (1999) Male grunts as mediators of social interaction with females in wild chacma baboons (*Papio cynocephalus ursinus*). *Behaviour* 136:221–242
- Pelletier F, Festa-Bianchet M (2004) Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, *Ovis canadensis*. *Behav Ecol Sociobiol* 56:546–551
- Powolny T (2012) Faire face à l'hiver—Quelles réponses à l'hétérogénéité de la ressource en agro-écosystème? L'exemple de l'alouette des champs (*Alauda arvensis*). Université de Poitiers, France
- Powolny T, Eraud C, Bretagnolle V (2012) Group size modulates time budget and foraging efficiency in captive skylarks *Alauda arvensis*. *J Ornithol* 153:485–490
- Powolny T, Bretagnolle V, Aguilar A, Eraud C (2014) Sex-Related Differences in the trade-off between foraging and vigilance in a granivorous forager. *PLoS ONE* 9(7):e101598. doi:10.1371/journal.pone.0101598
- Roberts G (1996) Why individual's vigilance declines as group size increases. *Anim Behav* 51:1077–1086
- Robinson RA, Sutherland WJ (1999) The winter distribution of seed-eating birds: habitat structure, seed density and seasonal depletion. *Ecography* 22:447–454

- Rohner C, Krebs CJ (1996) Owl predation on snowshoe hares: consequences of antipredator behaviour. *Oecologia* 108:303–310
- Rolando A, Caldoni R, De Sanctis A, Laiolo P (2001) Vigilance and neighbour distance in foraging flocks of red-billed choughs, *Pyrhcorax pyrrhcorax*. *J Zool Lond* 253:225–232
- Sansom A, Cresswell W, Minderman J, Lind J (2008) Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit? *Anim Behav* 75:1869–1875
- Schellinck J, White T (2011) A review of attraction and repulsion models of aggregation: methods, findings and a discussion of model validation. *Ecol Model* 222:1897–1911
- Steenbeck R, Piek RC, Van Buul M, Van Hoff JARAM (1999) Vigilance in wild Thomas's langurs (*Presbytis thomasi*): the importance of infanticide risk. *Behav Ecol Sociobiol* 45:137–150
- Teichroeb JA, Sicotte P (2012) Cost-free vigilance during feeding in folivorous primates? Examining the effects of predation risk, scramble competition, and infanticide threat on vigilance in ursine colobus monkeys (*Colobus vellerosus*). *Behav Ecol Sociobiol* 66:453–466
- Templeton JJ, Giraldeau LA (1995) Public information cues affect the scrounging decisions of starlings. *Anim Behav* 49:1617–1626
- Tisdale V, Fernandez-Juricic E (2009) Vigilance and predator detection vary between avian species with different visual acuity and coverage. *Behav Ecol* 20:936–945
- Treves A (1998) The influence of group size and neighbours on vigilance in two species of arboreal monkeys. *Behaviour* 135:453–481
- Treves A (2000) Theory and method in studies of vigilance and aggregation. *Anim Behav* 60:711–722
- Valone TJ (1993) Patch information and estimation—a cost of group foraging. *Oikos* 68:258–266
- Valone TJ, Templeton JJ (2002) Public information for the assessment of quality: a widespread social phenomenon. *Philos Trans R Soc Lond B* 357:1549–1557
- Verdolin JL (2006) Meta-analysis of foraging and predation risk trade-offs in terrestrials systems. *Behav Ecol Sociobiol* 60:457–464
- Whittingham MJ, Markland HM (2002) The influence of substrate on the functional response of an avian granivore and its implications for farmland bird conservation. *Oecologia* 130:637–644
- Whittingham MJ, Devereux CL, Evans AD, Bradbury RB (2006) Altering perceived predation risk and food availability: management prescriptions to benefit farmland birds on stubble fields. *J Appl Ecol* 43:640–650
- Wilson JD, Evans J, Browne SJ, King JR (1997) Territory distribution and breeding success of skylarks *Alauda arvensis* on organic and intensive farmland in southern England. *J Appl Ecol* 34:1462–1478
- Wrangham RW (1980) An ecological model of female bonded primate groups. *Behaviour* 75:262–300
- Zimmer C, Boos M, Poulin N, Gosler A, Petit O, Robin JP (2011) Evidence of the trade-off between starvation and predation risks in ducks. *PLoS ONE* 6:e22352