

Group size modulates time budget and foraging efficiency in captive Skylarks, *Alauda arvensis*

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Abstract Skylarks (*Alauda arvensis*) are known to adopt a typical aggregative behaviour during the wintering period. A further benefit is that individuals in larger groups can decrease the amount of time they spent being vigilant, while maintaining a high probability of predator detection. Using wild birds temporarily housed in outdoor aviaries, we investigated the influence of group size (1, 2 and 4 individuals) on individual time budget (vigilance vs. foraging), and the pecking (number of pecks) and intake rates (number of seeds consumed). Results showed that individuals reduced their vigilance and increased their pecking rate when group size increased. However, the intake rate was not maximised in the largest group suggesting that large flocks would negatively affect individual foraging efficiency. A consideration of the whole set of costs and benefits will be necessary before the adaptive value of group living in any species can be fully assessed.

Keywords *Alauda arvensis* · Group size · Time budget · Vigilance · Intake rate

Zusammenfassung

Gruppengröße beeinflusst den zeitlichen Aufwand und die Effizienz der Nahrungsaufnahme bei in Volieren gehaltenen Feldlerchen, *Alauda arvensis*

Feldlerchen (*Alauda arvensis*) sind für ihre typische Gruppenbildung während des Winters bekannt. Ein Vorteil dieses Verhaltens ist, dass innerhalb größerer Gruppen jedes einzelne Tier weniger Zeit dafür aufbringen muss, nach Feinden Ausschau zu halten, ohne dass dadurch die Chance leidet, Feinde frühzeitig zu entdecken. Mit zeitweise in Außenvolieren gehaltenen, wilden Vögeln untersuchten wir den Einfluss der Gruppengröße (1, 2 und 4 Individuen) auf den individuellen Zeitaufwand (Wachsamkeit vs. Nahrungsaufnahme), die Pick-Rate (Anzahl der Pickbewegungen) und die Nahrungsaufnahme (gemessen als Anzahl gefressener Körner). Die Ergebnisse zeigten, dass bei wachsender Gruppengröße die Einzeltiere ihre Wachsamkeit reduzierten und die Pick-Rate erhöhten. Aber die Nahrungsaufnahme war in der größten Gruppe nicht am größten, was nahe legt, dass große Gruppen die Effizienz der Nahrungsaufnahme der Einzeltiere negativ beeinflussen könnte. Eine komplette Kosten-Nutzen-Analyse ist notwendig, um für eine Tierart den adaptiven Wert der Gruppenbildung für ein Einzeltier vollständig zu erfassen.

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Introduction

Many animal species live in groups (Krause and Ruxton 2002), because of anti-predator effects such as risk dilution, predator confusion or corporate vigilance (Krebs and Davies 1996; Krause and Ruxton 2002), as well as the

improved resource exploitation (Valone and Templeton 2002) that grouping provides. Overall, living in groups significantly impacts the time budget of individuals, and in particular the amount of time that can be allocated to two often exclusive fitness-related activities: vigilance and foraging (Pulliam 1973; Elgar 1989; Lima 1990). Many studies have reported negative correlations between the time devoted to vigilance and the time spent foraging, as well as a reduction in predation risk through a group size effect (Barnard 1980; Bertram 1980; Elgar 1989; Lima 1995; Roberts 1995, 1996; Beauchamp 2008). However, while most studies have shown positive covariation between foraging time and group size, few have explicitly investigated whether group size may similarly modulate energetic gain (Cresswell 1994; Dolman 1995; Beauchamp 1998).

In this study, we investigated the effects of group size on both time budget and foraging efficiency simultaneously, using the Eurasian Skylark (*Alauda arvensis*) as a study model. Although Skylarks live in open farmland landscapes throughout the year, their life history differs between summer and winter. From being strongly territorial and feeding on insects in summer, Skylarks become highly gregarious in winter and rely on seeds and vegetative parts of plants.

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), we here used an experimental approach. Controlling for potential confounding factors such as food density, individual phenotype (body condition, sex) and weather, we experimentally modified captive Skylark group size in aviaries and measured time budget (devoted to vigilance and foraging) and foraging efficiency (i.e., pecking and intake rates).

Methods

Housing conditions

Wild Skylarks were trapped by mist-netting along the French Atlantic coast during their post-nuptial migration (October and November 2009; license number 2009–02). They were metal ringed, weighed (± 0.1 g) and their tarsus was measured using a digital calliper (± 0.01 mm). Birds were randomly assigned to groups of 10–12 individuals and acclimatised for 2 months in $4 \times 3 \times 2$ m ($l \times w \times h$) outdoor aviaries, located at the Centre d'Etudes Biologiques of Chizé, before the start of the experiment. Birds were fed ad libitum with a commercial seed mix, grit, oilseed rape and tapwater. Food was dispensed on a 2-m^2 synthetic green turf (height: 1 cm; density: 12 blades/cm²)

to accustom individuals to the experimental set-up (see below). Birds showing any sign of sickness were removed before entering the experiment. To limit the time spent under captive conditions and to have minimum influence on the birds, we released them into the wild during the pre-nuptial migration in early March. Experiments were carried out in compliance with French legal requirements and with the permission of the national conservation authority (no. 79/2002/D/06).

General experimental design

Experiments were carried out from 15 February to 12 March 2010 in outdoor aviaries of identical size and configuration than those used for acclimatisation. The night before each trial, all focal birds were weighed and deprived from food until the next morning. Trials were only performed under clear weather conditions and from 0900 to 1200 hours in order to avoid too long fasting periods.

In practice, Skylarks were placed 10 min before each trial in individual wire mesh cages ($50 \times 50 \times 40$ cm; mesh size: 1×1 cm) enabling visual contact among birds. Each cage was placed on a synthetic green turf on which 100 seeds were randomly scattered, corresponding to a density of 400 seeds/m², thus within the range of seed densities recorded in arable fields (Robinson and Sutherland 1999; Moorcroft et al. 2002). For our experiment, we used millet seeds (*Panicum miliaceum*) owing to their homogeneity in both colour (white) and size (mass = $0.007 \text{ g} \pm 0.0003$).

Nineteen focal individuals were tested for 3 group-sizes. A first group ($n = 5$ trials) was formed by the single focal individual. A second group ($n = 19$ trials) included a focal individual plus one conspecific (i.e. non-focal bird) and a third group ($n = 9$ trials) included a focal individual plus three conspecifics. Some individuals were tested in several group sizes. For the first group (focal subjects foraging alone), we minimised the number of solitary treatments because the birds showed behaviours that suggested high stress levels.

We used a total of 20 individuals in the focal group, in which only 4 birds were tested in the three different treatments, 5 birds in two different group sizes and 11 were tested in one group size only.

In our experimental design, we created two distinct groups: the first including only focal birds (20 birds) and the second group with only non-focal birds (18 birds). Flock composition was test-to-test randomised in order to avoid systematic association between focal and non-focal individuals and group sizes and testing conditions (temperature, date, hours, fasting duration).

Moreover, there were a maximum of 6 trials per day, but neither the focal nor the non-focal birds experienced more than one trial in any 1 day.

Non-focal birds were randomly assigned to each trial, and they were individually kept in identical wire mesh cages at a distance of 1 m from the focal individual. To avoid synchrony in behaviour (Fernandez-Juricic and Kacelnik 2004), non-focal birds were not provided with food during tests.

Data collection and analysis

Each focal observation lasted 5 min, starting when the first peck was recorded. Focal birds were video-recorded using a camcorder mounted on a tripod and set 1 m above the ground and about 1 m from bird. Videos were analysed using EthoLog 2.2 software (Ottoni 1996), and the number of pecks and time devoted to foraging and vigilance (in seconds) were quantified. A bird was considered to be vigilant when its head was above a horizontal line made by its body, and not orientated towards the ground. Conversely, birds were considered to be foraging when head was below the horizontal and actively scanning the ground or pecking (Whittingham and Markland 2002). The handling time, which represents the time needed to consume one prey item, and vigilance could not be separated given that Skylarks did not manipulate millet seeds and often adopted a vigilant posture when handling seeds. Even when the millet seeds had a husk, we found no empty husks after the tests, suggesting that skylarks minimised the handling of seeds before ingestion. Accordingly, handling time was assumed to be partly combined with vigilance.

In such a ground-feeding bird species, vigilance and foraging are considered to be mutually exclusive activities (Roberts 1996; Proctor et al. 2006), which were the only two behaviours considered in our study. At the end of each trial, seeds remaining on the green turf were collected to calculate food intake rate [expressed as the number of seeds consumed per unit of time (s)].

We used General Linear Mixed Models (GLMMs) to investigate whether pecking rate, intake rate and time budget were affected by group size. Group size was included as a fixed factor into the models. Because some focal individuals were tested for at least two group sizes, models were fitted with bird identity as a random factor. Our initial models also included the following individual covariates: date, average daily temperature, body condition (expressed as the residuals from a linear regression of body mass on tarsus length) and fasting duration (expressed in minutes, to account for the time of the morning at which each bird was tested). We started from complete models to obtain the minimally adequate model (Crawley 1993), following a backward stepwise model selection procedure, where the non-significant terms at $P = 0.05$ were sequentially removed. Pecking and intake rates were log-transformed and foraging time was arc-sin transformed to

ensure normality and homoscedasticity assumptions. All analyses were performed using Statistica 7.1. (SAS Institute). Means are expressed \pm SE.

Results and discussion

In Skylarks, group size significantly influenced time budget, with a larger proportion of time spent foraging in larger groups (Table 1). When focal individuals were alone, almost all the time-budget consisted in vigilance (i.e. 97%), despite the fact that these individuals had been fasting for 13 h (± 3 h). This suggested that individuals would favour immediate survival by maximising vigilance rather than by energy intake. This high proportion of time spent in vigilance for solitary birds is obviously energetically non-adaptive and could explain why wintering Skylarks are so rarely observed alone in the field (Powolny, personal observation). Interestingly, adding a single individual to the focal bird immediately resulted in an eightfold increase in the proportion of its time allocated to foraging (from 3 to 25%; Fig. 1a). This increase was even magnified when focal birds were surrounded by three conspecifics. Under such situation, feeding and vigilance each accounted for half of the time budget in the focal bird (Fig. 1a).

These results are in agreement with Pulliam's model (1973), which predicts that individuals can decrease their own anti-predator vigilance by taking advantage of vigilance from other group members without decreasing predator detectability (Roberts 1996; Bednekoff and Lima 1998). Although the increased feeding time is largely documented in the literature (Lima 1995; Beauchamp 2008), this study showed a spectacular increase in non-vigilant time by a simple addition of 3 conspecifics, especially for a species in which group size can reach several hundred individuals in winter. According to the *detection effect hypothesis* (Pulliam 1973), if the individuals of the group scan at random for predators, the probability of detecting a predator increases with group size. Therefore, individuals living in a group can reduce the proportion of time that they spend in vigilance and increase the time spent in other activities such as foraging, without increasing the risk of predation. However, Skylarks that forage in large groups do not necessarily receive the energetic benefit of an increase in collective vigilance. Indeed, our study confirms that increasing feeding time with larger group size translates into an increase in pecking rate (Cresswell 1994; Fernandez-Juricic et al. 2004; Fig. 1b). However, conversely to expectations (Fernandez-Juricic et al. 2004), seed intake rate did not increase as pecking rate did, particularly between groups of two and four birds (Fig. 1b).

According to Beauchamp (1998), a simple addition of three or four birds would be sufficient to double the intake

Table 1 Results from generalized linear mixed models testing the effects of group size, date, fasting duration and body condition on time spent foraging, pecking and intake rates in Skylark (*Alauda arvensis*)

Dependent variable	Fixed factor	df	F	P	r ²
Foraging time	Group size	2	44.9	<0.001	0.75
	Date	1	0.18	0.68	
	Fasting period	1	0	1	
	Body condition	1	0.23	0.64	
Pecking rate	Group size	2	21.3	<0.001	0.48
	Date	1	0.5	0.49	
	Fasting period	1	0.21	0.65	
	Body condition	1	0.05	0.81	
Intake rate	Group size	2	17.13	<0.001	0.60
	Date	1	0.00046	0.98	
	Fasting period	1	1.34	0.27	
	Body condition	1	0.37	0.55	

Group size was included as a fixed factor into the models. Models were fitted with bird identity as a random factor. Results from the full models can be provided. A backward selection procedure was used, with least significant variables being removed sequentially, until a minimum adequate model was reached in which all variables were retained at $P = 0.05$

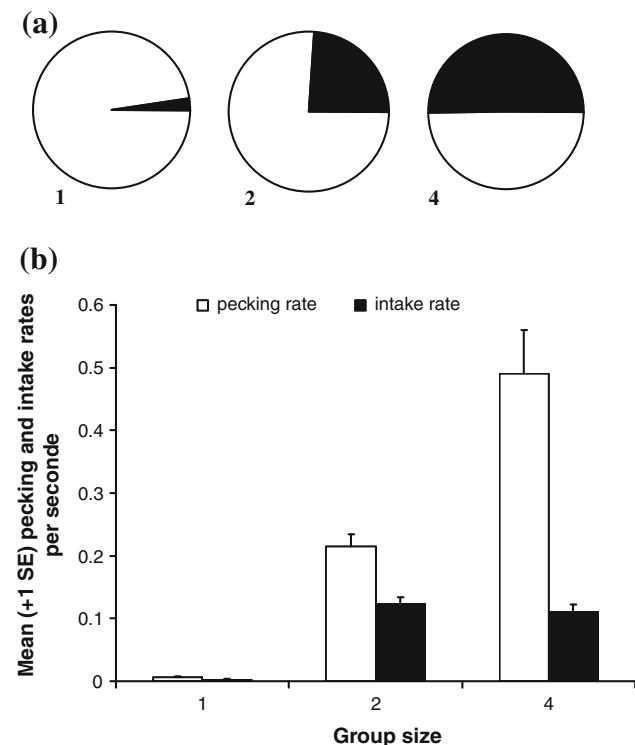


Fig. 1 **a** Changes in Skylark (*Alauda arvensis*) time budgets (black: foraging; white: vigilance) with different group sizes. 1 Single bird; 2 one focal bird and 1 conspecific; 4 one focal bird and 3 conspecifics. **b** Mean pecking (open bars, pecks/s) and intake (filled bars, seeds ingested/s) rates depending on Skylark group sizes. Vertical bars standard errors

rate of a solitary bird. In Skylark, adding a single bird to a solitary individual resulted in a 60-fold increase in intake rate, although the increase is not any longer visible with the addition of two supplementary birds. This intriguing result

was similarly documented in a shorebird, the Common Redshank (*Tringa totanus*). In agreement with Cresswell (1994), this discrepancy between pecking and intake rates might be the consequence of increased unsuccessful pecks with increasing group size. If true, this implicitly suggests that the increased foraging time associated with larger group sizes would have no clear energetic benefits.

By being not allowed to feed, non-focal birds may appear more vigilant and distract the attention of the focal birds. Moreover, by seeing companions in a head-up posture, the focal bird acquired social information on the dangerousness of the environment affecting de facto its own perception of risk. Even if these non-feeding birds may appear more vigilant and distract the attention of the focal birds, we observed that the focal birds spent more time in foraging activity. A previous study showed a similar result with Brown-headed Cowbirds (*Molothrus ater*) using feeding non-focal individuals (Fernandez-Juricic et al. 2007).

Among plausible hypotheses to explain this pattern, one is the *resource selectivity hypothesis* (Triplet 1994), in which an apparent decrease in feeding efficiency may result from an increased feeding selectivity, given that more time is available for feeding in larger groups. This was supported by a study on the Eurasian Oystercatcher (*Haematopus ostralegus*) feeding on mussels, where birds were shown to consume prey of different sizes according to the density of conspecifics (Triplet 1994; see also Triplet et al. 1999). However, this seems unlikely in our experimental study since we used seeds of equal mass and aspect, therefore avoiding any selective process. The second hypothesis is the *interference hypothesis*, which proposes that a decrease in intake rate with increased group size may

result from an increased interference among group members (Lima et al. 1999; Sansom et al. 2008). Specifically, the presence of coincidentally foraging individuals (*perceived competition*; Amita et al. 2009) may influence behaviour without any physical contacts. In this case, the simple presence of potential competitors, independently of their effect on resource density, can also induce a reduction in feeding rate (Vasquez and Kacelnik 2000; Johnson et al. 2001; Gauvin and Giraldeau 2004). In our experimental design, Skylarks could also reduce their feeding rates when in the company of competitors located in an adjacent cage that could not affect the food availability or interact with the forager. By being less vigilant, time would be allocated to competitive activities rather than for maximising intake rate (Stillman et al. 1997). Although our experimental design did not allow physical contacts, the high density of Skylarks (1 Skylark/m²) in the largest group may have negatively influenced individual behaviours through indirect interference (Schoener 1983), leading to more unsuccessful pecks. The differences observed between the pecking and intake rates could also be explained by the presence of companion, in which the decrease in vigilant time reflects scramble competition for limited resources (Clark and Mangel 1986; Elgar 1989). According to this idea, when a group size increases in a food-limited environment, animals consequently increase their feeding time (and feeding rate) in order to gain greater portion of the food supply, without direct interactions between group members. Increasing group size may impose an adaptive increase in feeding rate to allow individuals to maximise their share of the resource, and increased feeding rate may be achieved at the expense of vigilance. Consequently, the increased pecking rates may be induced by the increased perception of competition for the resource within the groups and may not be a direct product of safety benefits of foraging in groups. However, one major assumption of this hypothesis suggests that scramble competition have an effect in a food-limited environment, which is not the case for this study. Indeed, since the entirety of seeds was not consumed, a density of seeds of 400 seeds/m² does not appear to be limited.

Our results do not currently allow dissociating the *resource selectivity* or *interference hypotheses*, and further studies are clearly needed, especially regarding behavioural mechanisms of seed selectivity.

It should be stressed that, according to Beauchamp (1998), the contrasted relationship found between intake rate and group size may be partly explained by the differences between experimental and observational studies which often do not control for confounding factors (i.e. food density and temperature). One major finding of our study is the lack of relationships between pecking and intake rates, suggesting that, in this species, pecking rate

may not be an adequate *proxy* of food consumption, in contradiction with many previous studies that indifferently used pecking and intake rates (Morgan and Fernández-Juricic 2007).

Conservation considerations

In Europe, the populations of a suite of granivorous passerines including Skylarks have suffered a sustained decline for several decades (Fuller et al. 1995). Several studies suggested that this decline may be partly explained by a decrease in winter food availability and a concomitant reduction in survival (Chamberlain and Crick 1999).

Food availability directly affects the distribution of seed-eating species (Stephens et al. 2003). According to Robinson and Sutherland (1999), a positive relationship between seed and bird densities was shown in winter. Consequently, poor quality patches are generally avoided because they may have negative effects on energetic gains and relatedly on condition-dependant life history traits. Our findings suggest that the negative effects of low seed densities may be magnified at low group size. Indeed, in addition to scarce food resources, living in groups with few conspecifics implies a high vigilance rate at the expense of foraging. Hence, the low energy gain on poor patches may result from the cumulative effects of a lack of resources and the need for vigilance.

Alternatively, high quality patches generally held high bird densities (Stephens et al. 2003). However, our result suggests that intake rate may be negatively impacted by large group size by competition. Therefore, we wonder whether preserving or creating scarce, isolated and small rich habitats (i.e. cereal stubble; Robinson and Sutherland 1999) is a relevant conservation issue to maximise energy gains in wintering farmland birds.

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