



## Speed–accuracy trade-off and its consequences in a scramble competition context



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Animals foraging in groups commonly respond to the presence of others by increasing their foraging rate, an increase that could come at the expense of prey detection accuracy. Yet the existence and consequences of such so-called ‘speed–accuracy trade-offs’ in group-foraging animals remain unexplored. We used group-feeding zebra finches, *Taeniopygia guttata*, to determine how search speed affects food detection accuracy and how a potential speed–accuracy trade-off influences feeding success. We found significant between-individual differences in hopping speed as well as evidence that faster individuals were more likely to overlook food, demonstrating the existence of a trade-off between speed and food detection probability. We also found that feeding success was positively predicted by an individual’s food detection probability, whereas it was unrelated to hopping speed. These findings have several implications. First, they indicate that social animals, like solitary foragers, may be affected by perhaps universal constraints when foraging, such as limited attention. These constraints may contribute to promote between-individual variation in foraging tactics within social groups. Second, the existence of a speed–accuracy trade-off suggests that between-individual behavioural differences are more likely to come from differential allocation between speed and accuracy than from differences in general intrinsic abilities to exploit food resources. Finally, scramble competition’s outcomes are likely to be determined by a combination of foraging abilities that individuals must trade off against one another, calling for an integrative approach of how natural selection shapes interactive behavioural dimensions during foraging.

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Foraging theory assumes that resource exploitation behaviours have been moulded by natural selection to achieve maximum fitness gains (Giraldeau & Caraco, 2000; Stephens & Krebs, 1986). Resource exploitation decisions, such as patch residence time, prey choice or use of alternative foraging tactics, have been demonstrated in many cases to maximize the net rate of food intake (Giraldeau & Caraco, 2000; Stephens & Krebs, 1986). In a social context for example, increasing the speed of food searching, or food prospection, is thus thought to provide higher payoffs in a scramble competition (Shaw, Tregenza, Parker, & Harvey, 1995).

Evidence suggests, however, that individual behaviour can sometimes appear maladaptive or suboptimal often as a result of some cognitive constraints, and this may affect resource exploitation (Fawcett, Hamblin, & Giraldeau, 2013; Houston, McNamara, & Steer, 2007; Kacelnik, 2006). One major cognitive constraint on resource exploitation concerns an animal’s limited ability to devote attention to various sources of cues (Abbott & Sherratt, 2013; Dukas, 2002; Dukas & Kamil, 2001; Wang, Ings, Proulx, & Chittka, 2013). For instance, theoretical and experimental evidence suggests that limited attention can constrain search ability leaving foragers with two options: reduce search speed to attend to a wider range of potential targets and improve prey detection accuracy, or increase search speed but reduce attention to a few specific features of prey items (Gendron & Staddon, 1983; Reid & Shettleworth, 1992). Limited attention is therefore thought to result in a speed–accuracy trade-off, where the individual’s probability of

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detecting food or choosing profitable patches is negatively related to its search speed (Abbott & Sherratt, 2013; Chittka, Dyer, Bock, & Dornhaus, 2003; Chittka, Skorupski, & Raine, 2009; Janson & DiBitetti, 1997).

Such a speed–accuracy trade-off could have important consequences in group-foraging animals for several reasons: first, theoretical and experimental evidence shows that search speed, taken in isolation, is a good predictor of competition outcomes, with faster individuals usually showing a higher feeding success (Shaw et al., 1995). When foraging in the company of others, individuals may, however, be subject to conflicting demands, such as the need to increase feeding rate in response to competitors or reduce search rate to detect cryptic prey (Courant & Giraldeau, 2008). The extent to which these two options coexist within foraging groups remains unknown. Second, the study of speed–accuracy trade-offs has up to now focused on animals foraging alone (Chittka et al., 2003, 2009; Gendron, 1986; but see Janson & DiBitetti, 1997) and it remains unknown whether speed–accuracy trade-offs may also affect group-foraging animals and promote between-individual variation in foraging tactics (i.e. variation in search speed). Third, it remains possible that speed–accuracy trade-offs exist at the individual level (i.e. negative within-individual correlation between speed and accuracy, Fig. 1a, b; Chittka et al., 2003; Gendron & Staddon, 1983; Reid & Shettleworth, 1992) but not at the group level (i.e. between-individual correlation between speed and accuracy) if competitors do not differ in their foraging tactics but rather in their general intrinsic abilities to exploit food resources (a positive relationship between speed and accuracy may be expected in this case, Fig. 1b; see Van Noordwijk & De Jong, 1986). Testing for a between-individual relationship between search speed and prey detection accuracy in a scramble competition context is thus particularly relevant for predicting the emergence and coexistence of successful foraging abilities and tactics within populations.

In the present study we investigated the existence of a potential speed–accuracy trade-off at the group level (i.e. where the accuracy of various birds differing in search speed is examined) and its consequences for feeding success in a scramble competition context using flocks of group-feeding zebra finches, *Taeniopygia guttata*. Flocks of four birds were allowed to forage from dispersed patches of seeds on a foraging grid for several consecutive trials during two consecutive experimental sessions, between which the group composition changed. First, we looked for the existence of between-individual differences in foraging behaviour and then asked whether an individual's hopping speed affected its accuracy as estimated by the probability of detecting a patch of seeds. If

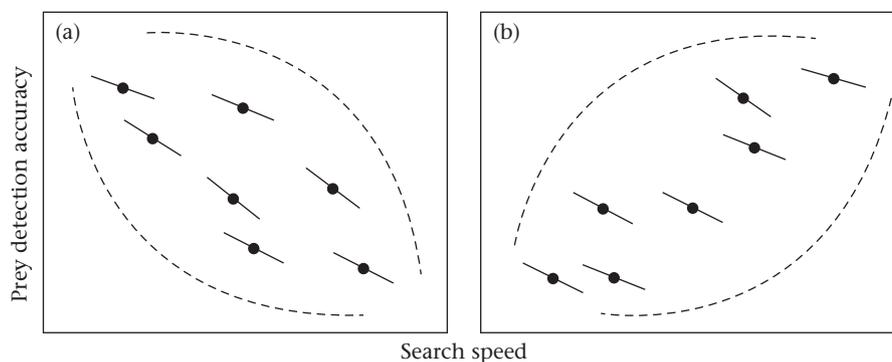
zebra finches exhibit a speed–accuracy trade-off at the group level, then we expected that the faster birds would be less efficient at locating seed clumps than slower birds. Ground-feeding birds competing for dispersed food typically adopt two alternative tactics, producing and scrounging, that involve different means of searching for food (Barnard & Sibly, 1981). To control for any confounding effect of the use of both producer and scrounger foraging tactics on the probability of detecting seed patches, the investment in each tactic was quantified using the number of hops with head up or down (Coolen, Giraldeau, & Lavoie, 2001; Wu & Giraldeau, 2005). We expected individuals using the scrounger tactic more, thus hopping more with the head up, to overlook more seed-containing wells. Finally, we investigated the relationship between accuracy, hopping speed and feeding success, estimated as the total seeds eaten, to evaluate the benefits associated with varying foraging behaviours in a social context.

## METHODS

### Study Subjects

We purchased 15 male and 15 female zebra finches from a local supplier (L'oisellerie de l'Estrie, Québec, Canada). The zebra finch is a small monogamous Australasian ground-feeding bird which is highly gregarious outside reproduction periods (Zann, 1996). It generally forages in flocks, is easy to breed and to maintain in captivity and is commonly used in foraging studies (Beauchamp, 2006; David & Giraldeau, 2012; Giraldeau, Hogan, & Clinchy, 1990).

Outside experimental periods, birds were kept in unisex groups of two to three individuals in home cages (52 × 29 cm and 38 cm high) containing two feeders, two white water dispensers and four perches, in rooms with lights reflecting the natural spectrum. Groups were monitored and cared for every day. Zebra finches are docile birds and no signs of overt aggression, dominance or distress were observed throughout the experiments. Millet seeds, water and cuttlebones were provided ad libitum while vegetables and hardboiled egg mixture were occasionally offered. Room temperature was maintained at 24 ± 1 °C on a 12:12 h light:dark cycle (0800–2000 hours Eastern Daylight Savings Time [EDST]). Each individual wore an orange numbered plastic leg ring (AC Hughes, Hampton Hill, U.K., size XF) allowing individual identification. After the experiments, birds were returned to their home cage in groups of two to three individuals to be used for subsequent experiments. Fishing nets were used to catch and transport individuals from rooms. All procedures complied with guidelines from the Canadian



**Figure 1.** Hypothetical relationships between prey detection accuracy and search speed. Average individual behaviour and intraindividual variability are represented by, respectively, points and lines crossing these points. Dashed lines represent the general between-individual correlation patterns. (a) Potential trade-off between prey detection accuracy and search speed at the group level. (b) Prey detection accuracy and search speed are positively related at the group level, owing to individual differences in general intrinsic abilities to exploit food resources (Van Noordwijk & De Jong, 1986). We assumed that prey detection accuracy and search speed are negatively related at the within-individual level in both cases.

Council for Animal Care and were approved under protocol O210-676-0211 of the UQAM committee for animal care.

### Foraging Trials

We measured each individual's foraging behaviours in two experimental sessions: a different unisex flock of either four males or four females was used in each session. Each experimental session was conducted over 3 consecutive days. We used unisex flocks to avoid any interference from sexual activities during foraging trials. For the purpose of another study (David, Cézilly, & Giraldeau, 2011), the birds had been sorted within groups according to their exploration tendencies, with each flock composed of a high-, a medium- and a low-exploratory bird, plus a fourth one whose exploration behaviour was unknown. However, exploration tendencies had no effect on hopping speed ( $\chi^2_1 = 1.10$ ,  $P = 0.29$ ; Spearman  $r_s = 0.01$ ) or on prey detection probability ( $\chi^2_1 = 1.32$ ,  $P = 0.25$ ; Spearman  $r_s = -0.02$ ). We did not place birds from the same home cage in the same foraging flock to avoid any effect of familiarity. Birds were given 1 week to rest after the first experimental session, after which they were assorted into a different same-sex foraging flock, again using birds that had not been together before. However, it was impossible to form three same-sex flocks in the second session with a totally different composition from that in the first session, so we introduced three new males and three new females in the second session. Nevertheless, owing to a lack of available birds, two individuals were tested together in the same flock in both sessions. Also, we omitted the data from one individual on one trial because when on the foraging grid, it spent its time chasing flockmates without much foraging activity. Similarly, we omitted data from another individual that only spent a few seconds on the foraging grid during the whole experiment without eating a single seed. Therefore our final sample size was 28 different individuals.

The 3 days within each experimental session were used to familiarize the individuals with the foraging grid (day 1), train individuals (day 2) and finally test individual foraging behaviour (day 3). On the first day of each session, each bird was banded with a unique combination of blue and light blue leg rings for identification from the video footage. Thus, in addition to their orange identification ring, the four birds in each flock wore one of the following colour combinations: light blue–light blue, light blue–blue, blue–light blue and blue–blue. Blue and light blue have no effect on agonistic between-individual interactions or foraging behaviour (David, Auclair, & Cézilly, 2011). Birds were then placed with their flockmates in a large indoor aviary (3.8 × 1.5 m and 2.3 m high) containing two tables which together supported a light grey foraging grid with 64 unpainted wells (1.6 cm in diameter and 1 cm deep) spaced every 8.1 cm, two perches and two water dispensers. The aviaries were kept on the same light cycle and temperature as the holding room. In order for the birds to familiarize themselves with the aviary and the foraging grid, each well was filled with millet seeds on the first day.

The second day of each session corresponded to a training phase using the same conditions as the test phase so that birds could become familiar with the experimental conditions. The grid and the aviary floor were cleaned and birds were deprived of food for 1 h. After that, each flock was provided with 50 white millet seeds distributed in 10 randomly selected wells with five seeds per well. This procedure was repeated every hour for seven consecutive trials. Water remained accessible ad libitum throughout the day. After the final trial, birds had ad libitum access to seeds dispersed on the foraging grid until the next morning.

The third day of each session corresponded to the test phase which was similar to the training phase except that only five trials

were conducted and each was videotaped for further analyses. Following the fifth and final trial, the birds were returned to their home cages and provided with ad libitum access to seed and water.

### Video Analyses

Data were collected from the first three trials of the third day of each session, which is sufficient to provide a reliable estimate of food-searching behaviour, and minimizes the risk of quantifying behaviour when birds are satiated or nearly so. During video analyses we recorded for each bird the number of hops it performed on the foraging grid. Based on an imaginary line extending from a bird's eyes and passing through its nares we noted whether it was hopping with this line pointing above the horizontal (hereafter referred to as 'hops with the head up'), and the number of hops performed with the line pointing below the horizontal (hereafter referred to as 'hops with the head down'; Coolen et al., 2001; Wu & Giraldeau, 2005). It has previously been demonstrated in zebra finches and in a closely related estrildid species, the nutmeg mannikin, *Lonchura punctulata*, that the proportion of hops with the head up indicates a bird's investment in the scrounger tactic (Wu & Giraldeau, 2005) while hops with the head down indicate the investment in the producer or food-searching tactic (Coolen et al., 2001). For each bird we measured the total time it foraged on the grid, the number of seed-containing wells that it discovered (i.e. produced), and the number of seed-containing wells that it joined after they had been discovered and were being exploited by flockmates (i.e. scrounged). The seeds ingested by a given individual can easily be recorded as zebra finches perform highly stereotypic bill movements when separating the seed from the husk (Zann, 1996). In most cases, the husk can be seen falling from the bill, indicating that a seed has been eaten. Using this behaviour we counted the seeds a bird ate from produced and scrounged wells. We computed the total number of seeds eaten as the sum of the number of seeds produced and scrounged for each bird in each trial. For all trials we stopped the analysis when the last undiscovered well had been found and all its seeds had been consumed. Search speed was computed as the number of hops performed on the foraging grid divided by time spent on it (hereafter called 'hopping speed'). Here we make the assumption that the distance covered through a single hop does not differ between individuals.

To assess the probability of detecting prey we counted the seed-containing wells that were overlooked by a bird as it hopped on the grid. To do so we divided the foraging grid into 49 virtual squares each corner of which corresponded to a well position (Fig. 2) so that each square encompassed four wells. A seed-containing well was considered to have been overlooked when a bird moved out of a square that encompassed it. However, if a bird passed through two squares that shared a seed-containing well, this well was only deemed overlooked when the forager left the second square without having discovered the shared seed-containing well (Fig. 2). The probability of detection was thus computed for each bird in each trial as the number of seed-containing wells discovered, divided by the sum of seed-containing wells discovered and seed-containing wells overlooked. We did not incorporate a measure of incorrect detections in this computation as in no instances did birds attempt to feed from an empty well.

### Data Analyses

All statistical analyses were carried out using the statistical freeware R-2.14.1 (R Development Core Team, 2012). Since we had repeated measurements on each individual's behaviour within two different experimental sessions, we investigated behavioural consistency both within and between sessions by calculating the



**Figure 2.** Schematic representation of the foraging grid. Adjacent squares share two wells. If seeds are present in one of the two wells shared by A and B and if the bird hops consecutively through A and B, then it will be considered to have overlooked them only when entering square C (see *Methods* for more details). If the bird passes through square B only, it will be deemed to have overlooked the seed-containing well when entering C.

repeatability of each behaviour using the ‘rptR’ package (Nakagawa & Schielzeth, 2010). Hopping speed consistency was computed using anova-based repeatability for Gaussian data. The consistencies of both the number of hops and the number of seeds eaten were computed using link scale repeatability for count data, except for consistency of the number of seeds eaten in the second session with the overdispersion parameter falling below 1. Since underdispersion may lead to erroneous estimation of the 95% confidence interval (CI) and because data were normally distributed for this model (Shapiro test:  $P > 0.05$ ), we ran an anova-based analysis. Here we report the estimates (repeatability coefficient ( $R$ ) and 95% credible interval, CrI) of multiplicative overdispersion generalized linear mixed models (GLMM). The consistencies of proportion of hops with head up and probability of detection were computed using link scale repeatability for proportion data. For these variables we report the estimates ( $R$  and 95%CrI) of additive overdispersion GLMM-based models; note that these Bayesian methods do not provide any  $P$  value but only a 95%CrI (Nakagawa & Cuthill, 2007; Nakagawa & Schielzeth, 2010). Across-session behaviour repeatabilities were estimated using the between-individual covariance of a given behaviour across sessions using additive overdispersion GLMMs with Markov chain Monte Carlo estimation (Dingemans & Dochtermann, 2013).

To test the effects of hopping speed and proportion of hops with the head up on the probability of detecting seed-containing wells, we ran GLMMs and linear mixed models (LMM) using the lme4 package in R (Pinheiro & Bates, 2000) fitted with ‘individual identity’ nested within ‘flock’ as a random intercept factor. This procedure allowed us to take into account within- and between-session repeated measures for the same individual. All GLMMs were also fitted with a random slope for all covariates in the model as recommended by Schielzeth & Forstmeier (2009). The minimum adequate model was obtained by backward stepwise term deletion of nonsignificant variables ( $P < 0.05$ ; Crawley, 2002; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We investigated the probability of seed-containing well detection according to both hopping speed and the proportion of movements with the head up through a GLMM with a binomial error structure and logit link function. The model included the detection probability as the response variable, and hopping speed, the proportion of hops with head up and their interaction as covariates. However, more accurate birds may be

expected to find and eat more seeds, then spend less time hopping, and appear to search for food at a lower speed. This situation may generate a spurious negative relationship between hopping speed and detection probability. To investigate this possibility we ran the same model as above where the fixed factor ‘hopping speed’ was replaced with a modified ‘adjusted hopping speed’ variable. Adjusted hopping speed was computed as the number of hops performed on the foraging grid divided by time spent on it from which 1 s per seed ingested by the focal bird was subtracted. This allowed us to control arbitrarily for the time periods when birds were not actually hopping on the grid in the computation of hopping speed.

The influence of proportion of hops with the head up on hopping speed was independently investigated through an LMM. The model included hopping speed as the response variable and the proportion of hops with head up as a covariate.

We investigated the number of seeds eaten (produced and scrounged) according to hopping speed and the proportion of hops with the head up, and according to the detection probability, in two separate models to avoid collinearity between predictors (Zuur, Ieno, & Elphick, 2010). In all analyses we provide Spearman correlation coefficients or Spearman partial correlation coefficients as estimates of effect size (Cassey, Ewen, Blackburn, & Møller, 2004; Nakagawa & Cuthill, 2007; Zar, 2010).

## RESULTS

### *Individuals Consistent Within but Not Across Sessions*

The median number of hops per trial and per individual was 59 (range 11–266; interquartile range 38.5–85.3), and the median proportion of hops with the head up was 0.42 (range 0.04–0.77; interquartile range 0.27–0.54). The median number of seeds eaten per individual and per trial was 11 (range 0–31; interquartile range 7.8–14.0). The median number of seed-containing wells discovered per individual and per trial was 3 (range 0–9; interquartile range 2–5), while the median number of seed-containing wells overlooked was 1 (range 0–6; interquartile range 0–2) per trial and per individual. Overall, the recorded variables were found to be repeatable within the same session (i.e. in the same foraging flock). Repeatability estimates are summarized in Table 1. Between sessions (i.e. across different foraging flocks), repeatability estimates were found to be nonsignificant (note that the 95% credible intervals for all of the between-session estimates overlap zero).

### *Evidence for a Speed–Accuracy Trade-off*

The probability of detection was negatively influenced by both hopping speed ( $\chi^2_1 = 10.03$ ,  $P = 0.002$ , partial  $r_s = -0.40$ ; Fig. 3a) and the proportion of hops with the head up ( $\chi^2_1 = 9.88$ ,  $P = 0.002$ , partial  $r_s = -0.29$ ; Fig. 3b), but not by their interaction ( $\chi^2_1 = 0.10$ ,  $P = 0.75$ ). These effects still held when ‘adjusted hopping speed’ (see *Methods*) was used as a fixed factor (adjusted hopping speed:  $\chi^2_1 = 5.98$ ,  $P = 0.014$ , partial  $r_s = -0.34$ ; proportion of hops with the head up:  $\chi^2_1 = 11.11$ ,  $P < 0.001$ , partial  $r_s = -0.28$ ). The influence of hopping speed and proportion of hops with the head up did not vary across the two experimental sessions (interaction session\*hopping speed:  $\chi^2_1 = 1.07$ ,  $P = 0.30$ ; interaction session\*proportion of hops with the head up:  $\chi^2_1 = 0.01$ ,  $P = 0.92$ ). The proportion of hops with the head up had no influence on hopping speed ( $\chi^2_1 = 0.59$ ,  $P = 0.44$ , Spearman  $r_s = 0.07$ ). Thus, the faster the birds searched for seed-containing wells on the foraging grid, the more they were likely to overlook them. Similarly, the more they hopped with the head up, the more they were likely to overlook seed-containing wells.

**Table 1**  
Repeatability estimates ( $R$ ) of the recorded variables both within and between sessions

Behaviour	First session			Second session			Between sessions	
	$R$	95%CI or CrI	$P$	$R$	95%CI or CrI	$P$	$R$	95%CrI
Number of hops	0.31	[0.03, 0.58]	0.02	0.33	[0.04, 0.57]	<0.01	0.09	[-0.40, 0.46]
Proportion of hops with head up	0.09	[0.03, 0.15]	—	0.10	[0.06, 0.21]	—	0.23	[-0.20, 0.66]
Number of seeds ingested	0.50	[0.19, 0.71]	0.001	0.57	[0.34, 0.80]	<0.0001	0.22	[-0.21, 0.62]
Hopping speed	0.27	[-0.03, 0.56]	0.02	0.37	[0.09, 0.64]	<0.01	0.04	[-0.35, 0.42]
Probability of detection	0.18	[0.07, 0.40]	—	0.08	[0.03, 0.33]	—	0.54	[-0.33, 0.85]

95%CI or CrI: 95% confidence intervals (CI) or credible intervals (CrI) are shown. Confidence intervals are given for the first and second sessions where  $P$  values are also provided, and credible intervals for the between-sessions column, and in the first and second sessions where no  $P$  value is provided. Estimates obtained from proportion data and between-session data are computed using Bayesian methods that do not provide a  $P$  value (see [Methods](#)).

### Determinants of Feeding Success

Feeding success, taken as the number of seeds eaten per trial, was affected by the probability of detection ( $\chi^2_1 = 6.60$ ,  $P = 0.010$ , Spearman  $r_s = 0.27$ ; [Fig. 4a](#)). It was not, however, affected by hopping speed ( $\chi^2_1 = 0.44$ ,  $P = 0.51$ , Spearman  $r_s = -0.10$ ; [Fig. 4b](#)) or the proportion of hops with the head up ( $\chi^2_1 = 0.78$ ,  $P = 0.38$ , Spearman  $r_s = -0.24$ ; [Fig. 4c](#)). Thus, birds with a higher probability of detecting seed-containing wells ate more seeds, whereas feeding success was unrelated to hopping speed.

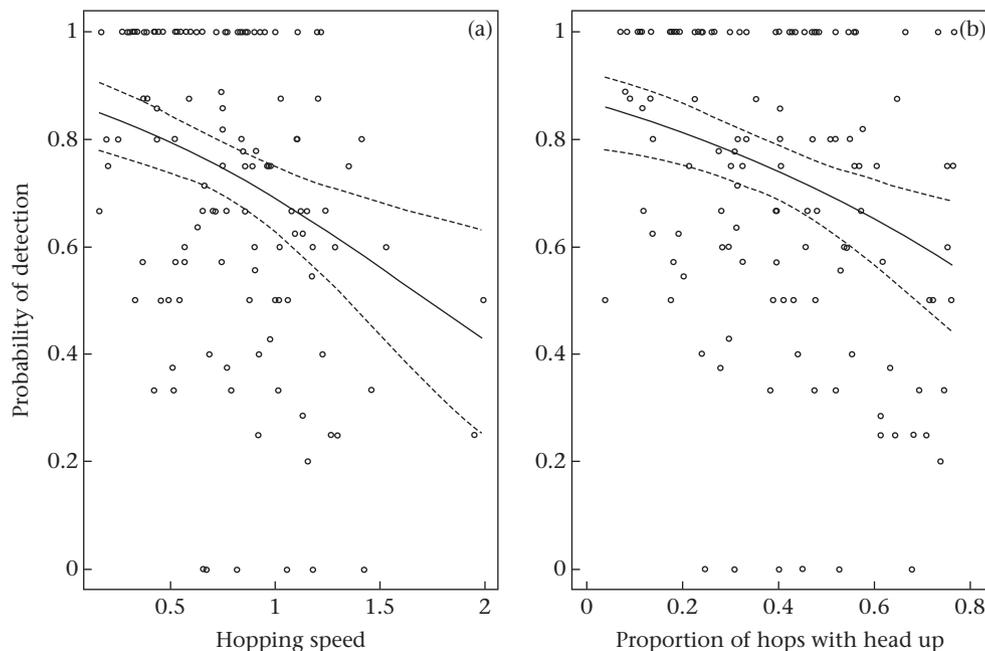
### DISCUSSION

Our study provides evidence for the existence of a speed–accuracy trade-off at the group level in a scramble competition context in zebra finches. Although most of the previous studies that found a speed–accuracy trade-off were performed with animals foraging alone ([Chittka et al., 2009](#); but see [Janson & DiBitetti, 1997](#)), our findings indicate that social animals may be affected by similar, and perhaps universal, constraints when foraging. In addition, a negative between-individual relationship between hopping speed and detection accuracy suggests that between-individual behavioural differences are more likely to come from

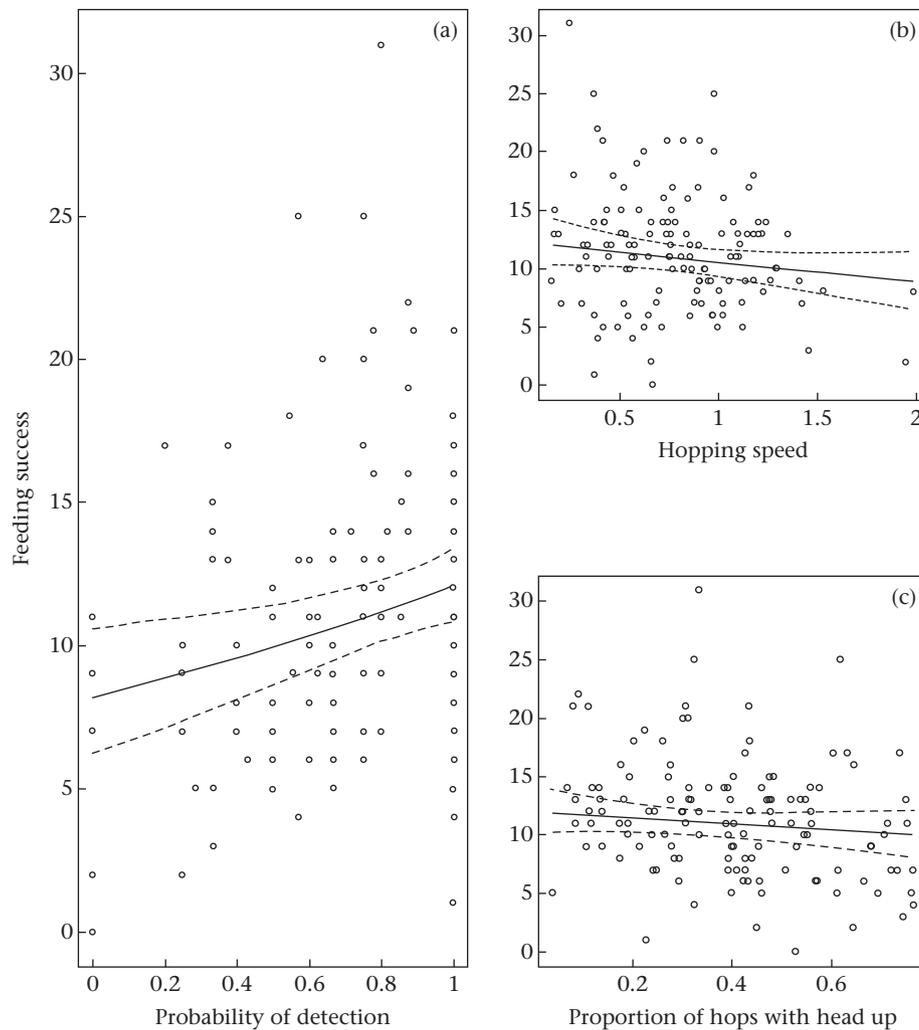
differential allocation between speed and accuracy than from differences in general intrinsic abilities to exploit food resources (see [Van Noordwijk & De Jong, 1986](#)). Overall, our findings call for an integrative study of the evolution of phenotypic traits in order to identify the selection pressures shaping different but possibly interactive dimensions of a phenotype ([Lailvaux & Kasumovic, 2011](#)).

### Behavioural Repeatability

Our within-subject design enabled us to assess within- and between-flock consistency of hopping speed and food detection probability. Hopping speed was found to be repeatable within sessions, indicating that birds displayed significant between-individual differences in their food-searching behaviour. Computed repeatability estimates are lower but comparable to the estimate computed in Bell et al.'s meta-analysis under the 'foraging' heading ( $R \sim 0.45$ ) ([Bell, Hankinson, & Laskowski, 2009](#)). However, it is noteworthy that hopping speed was not repeatable across the two experimental sessions (i.e. in flocks differing in their social composition). The distinction between within- and between-flock consistency is reminiscent of previous findings in zebra finches, that changes in the social composition of the foraging flock may



**Figure 3.** Effect of (a) hopping speed and (b) proportion of hops with head up on the probability of detecting seed-containing wells. Each point represents an individual's behavioural value in a given trial. The bold and dashed lines are, respectively, the regression line and its 95% confidence interval.



**Figure 4.** Influence of (a) the probability of detecting seed-containing wells, (b) hopping speed (controlling for proportion of hops with the head up) and (c) proportion of hops with the head up (controlling for hopping speed) on feeding success. Feeding success corresponds to the number of seeds eaten per trial per individual (i.e. produced and scrounged). Each point represents an individual's behavioural value in a given trial. The bold and dashed lines are, respectively, the regression line and its 95% confidence interval.

impair behavioural consistency (David, Cézilly, et al., 2011). However, note that within-session trials were performed during a single day whereas between-session trials were conducted at a 1-week interval. These different time lags may explain why within-session repeatabilities were found to be significant whereas between-session ones were not (Bell et al., 2009).

We found that detection probability was significantly but weakly repeatable within sessions. This finding is not very surprising as only 16% of the wells (10 out of 64) of the foraging grid were filled with seeds. Thus, small absolute differences in the number of overlooked wells may have translated into important relative differences between trials with large effects on the computed detection probability. We think that it would be misleading to conclude here that individuals show important differences in their ability to detect clumps of seeds that are hard to find, although similar findings have been reported elsewhere in the same species (Beauchamp, 2006).

#### *Speed–Accuracy Trade-off and the Evolution of Foraging Skills*

The probability of detecting seed-containing wells was found to be negatively related to both hopping speed and proportion of hops with the head up. We suggest that birds that mostly use the scrounger tactic have a lower probability of detection as they are

not actively searching for food but for conspecifics that have just discovered patches. Moreover, we are confident that the effect of hopping speed on detection probability is not confounded by scrounging behaviour as the interaction between detection probability and proportion of hops with the head up was not significant in our model, and hopping speed was not correlated with the proportion of hops with the head up. In addition, the significant influence of adjusted hopping speed (i.e. hopping speed controlled for time periods when birds were feeding, thus not moving) rules out the possibility that more accurate birds artificially appear as slower at searching for food (see Methods). The existence of a trade-off suggests that the payoffs associated with increasing search speed in a scramble competition (Beauchamp, 2006; Shaw et al., 1995) may be reduced by a lower probability of detecting clumps of seeds. A likely mechanism underlying the relationship between search speed and detection accuracy may be limited attention (Abbott & Sherratt, 2013; Chittka et al., 2009; Dukas, 2002; Gendron & Staddon, 1983) but further research would be required to determine its exact cause. The existence of this trade-off suggests that the optimal exploitation of feeding resources is not likely to rely on a single behavioural dimension that competitors may try to maximize but rather involves a compromise among several abilities that individuals must trade off. However, the extent to which this reduction in detection accuracy through increasing

search speed arises in the presence of competitors versus when foraging alone deserves further investigation.

#### *Speed–Accuracy Trade-off and Feeding Success*

We found that hopping speed taken alone was not a significant predictor of feeding success. The present result differs from previous findings in bumblebees, *Bombus terrestris*, which showed that fast-searching individuals enjoyed a higher nectar collection rate than slower individuals (Burns, 2005) and that the accuracy of choices among flowers was not related to nectar collection rate. However, the probability of detecting seed-containing wells positively predicted feeding success in the present study. Thus, we could expect competitors to decrease their hopping speed across trials, or at least to maximize, at any given hopping speed, their ability to detect patches of food. However, hopping speed did not predict feeding success so that fast foragers were rewarded with similar payoffs as slower foragers. The trade-off between search speed and detection accuracy is thus likely to be partly shaped by natural selection, where the maximization of detection accuracy is constrained by, supposedly, limited attention, and where sampling fast and superficially and sampling slow and thoroughly represent two extremes of a continuum of successful foraging tactics (Chittka et al., 2009). It follows that search speed alone is not the only relevant skill for successfully exploiting resources in a scramble competition context (Shaw et al., 1995). Instead, search accuracy is as important in determining subsequent individual feeding success (Courant & Giraldeau, 2008).

The trade-off between hopping speed and probability of detection may contribute to explaining why between-individual differences in search speed are maintained. Indeed, whereas low hopping speed is associated with a higher probability of detecting prey, high hopping speed could increase the encounter rate with profitable patches. Further experiments in which food spatial distribution varies between trials may help to investigate this possibility. Between-individual differences in hopping speed may also be maintained because it pays to search for food superficially when others search thoroughly (for instance when food is highly dispersed), and vice versa. The extent to which variation in search speed can thereby be maintained by frequency-dependent processes within foraging flocks deserves further investigation. The selection pressures acting on search speed and accuracy are also likely to vary depending on environmental stochasticity, clumpiness of resources, patches' profitability and so on (Gendron & Staddon, 1983). Assessing the relationships between payoffs, variation in search speed and prey detection accuracy is crucial to identify the selection pressures shaping the ability of social animals to exploit food resources.

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#### **References**

Abbott, K. R., & Sherratt, T. N. (2013). Optimal sampling and signal detection: unifying models of attention and speed–accuracy trade-offs. *Behavioral Ecology*, *24*, 605–616.

- Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour*, *29*, 543–550.
- Beauchamp, G. (2006). Phenotypic correlates of scrounging behavior in zebra finches: role of foraging efficiency and dominance. *Ethology*, *112*, 873–878.
- Bell, A., Hankinson, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, *77*, 771–783.
- Burns, J. G. (2005). Impulsive bees forage better: the advantage of quick, sometimes inaccurate foraging decisions. *Animal Behaviour*, *70*, e1–e5.
- Cassey, P., Ewen, J. G., Blackburn, T. M., & Møller, A. P. (2004). A survey of publication bias within evolutionary ecology. *Proceedings of the Royal Society B: Biological Sciences*, *271*, S451–S454.
- Chittka, L., Dyer, A. G., Bock, F., & Dornhaus, A. (2003). Bees trade off foraging speed for accuracy. *Nature*, *424*, 388.
- Chittka, L., Skorupski, P., & Raine, N. E. (2009). Speed–accuracy trade-offs in animal decision making. *Trends in Ecology & Evolution*, *24*, 400–407.
- Coolen, I., Giraldeau, L.-A., & Lavoie, M. (2001). Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. *Animal Behaviour*, *61*, 895–903.
- Courant, S., & Giraldeau, L.-A. (2008). Conspecific presence makes exploiting cryptic prey more difficult in wild-caught nutmeg mannikins. *Animal Behaviour*, *75*, 1101–1108.
- Crawley, M. (2002). *Statistical computing: An introduction to data analysis using S-plus*. Chichester, U.K.: Wiley.
- David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour*, *81*, 219–224.
- David, M., Cézilly, F., & Giraldeau, L.-A. (2011). Personality affects zebra finch feeding success in a producer-scrounger game. *Animal Behaviour*, *82*, 61–67.
- David, M., & Giraldeau, L.-A. (2012). Zebra finches in poor condition produce more and consume more food in a producer-scrounger game. *Behavioral Ecology*, *23*, 174–180.
- Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*, 39–54.
- Dukas, R. (2002). Behavioural and ecological consequences of limited attention. *Philosophical Transactions of the Royal Society B of London, Series B: Biological Sciences*, *357*, 1539–1547.
- Dukas, R., & Kamil, A. C. (2001). Limited attention: the constraint underlying search image. *Behavioral Ecology*, *12*, 192–199.
- Fawcett, T. W., Hamblin, S., & Giraldeau, L.-A. (2013). Exposing the behavioral gambit: the evolution of learning and decision rules. *Behavioral Ecology*, *24*, 2–11.
- Gendron, R. P. (1986). Searching for cryptic prey: evidence for optimal search rates and the formation of search images in quail. *Animal Behaviour*, *34*, 898–912.
- Gendron, R. P., & Staddon, J. E. R. (1983). Searching for cryptic prey: the effect of search rate. *American Naturalist*, *121*, 172–186.
- Giraldeau, L.-A., & Caraco, T. (2000). *Social foraging theory*. Princeton, U.K.: Princeton University Press.
- Giraldeau, L.-A., Hogan, J. A., & Clinchy, M. J. (1990). The payoffs to producing and scrounging – what happens when patches are divisible. *Ethology*, *85*, 132–146.
- Houston, A. I., McNamara, J. M., & Steer, M. D. (2007). Do we expect natural selection to produce rational behaviour? *Philosophical Transactions of the Royal Society, Series B: Biological Sciences*, *362*, 1531–1543.
- Janson, C. H., & DiBitetti, M. S. (1997). Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. *Behavioral Ecology and Sociobiology*, *41*, 17–24.
- Kacelnik, A. (2006). Meanings of rationality. In S. Hurley, & M. Nudds (Eds.), *Rational animals?* (pp. 87–105). Oxford, U.K.: Oxford University Press.
- Lailvaux, S. P., & Kasumovic, M. M. (2011). Defining individual quality over lifetimes and selective contexts. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 321–328.
- Nakagawa, S., & Cuthill, I. C. (2007). Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, *82*, 591–605.
- Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, *85*, 935–956.
- Pinheiro, J. C., & Bates, D. M. (2000). *Mixed-effects models in S and S-PLUS*. New York: Springer.
- R Development Core Team. (2012). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reid, P. J., & Shettleworth, S. J. (1992). Detection of cryptic prey: search image or search rate. *Journal of Experimental Psychology: Animal Behavior Processes*, *18*, 273–286.
- Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology*, *20*, 416–420.
- Shaw, J. J., Tregenza, T., Parker, G. A., & Harvey, I. F. (1995). Evolutionarily stable foraging speeds in feeding scrambles. A model and an experimental test. *Proceedings of the Royal Society B: Biological Sciences*, *260*, 273–277.
- Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton, NJ: Princeton University Press.
- Van Noordwijk, A. J., & De Jong, G. (1986). Acquisition and allocation of resources – their influence on variation in life-history tactics. *American Naturalist*, *128*, 137–142.
- Wang, M.-Y., Ings, T. C., Proulx, M. J., & Chittka, L. (2013). Can bees simultaneously engage in adaptive foraging behaviour and attend to cryptic predators? *Animal Behaviour*, *86*, 859–866.

- Wu, G. M., & Giraldeau, L.-A. (2005). Risky decisions: a test of risk sensitivity in socially foraging flocks of *Lonchura punctulata*. *Behavioral Ecology*, 16, 8–14.
- Zann, R. A. (1996). *The zebra finch: A synthesis of field and laboratory studies*. Oxford, U.K.: Oxford University Press.
- Zar, J. H. (2010). *Biostatistical analysis* (5th ed.). Upper Saddle River, NJ: Pearson Education.
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.
- Zuur, A., Ieno, E., Walker, N., Saveliev, A., & Smith, G. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.