

Foraging, Fear and Behavioural Variation, a Lesson from Hum-Mingbirds

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Abstract: Traditionally, foraging behaviour has been explained as the response to a trade-off between energetic gain from feeding resources and the potential costs from concomitant risks. However, increasing number of studies has shown that this view fail to explain an important fraction of the variation in foraging across a variety of taxa. One of potential mechanisms that may account for this variation is that various behaviours associated with foraging may have different fitness consequences and that may further depend on the environmental context. Here, we explored this mechanism by evaluating foraging efficiency of Long-billed Hermit hummingbirds (*Phaethornis longirostris*) with regard to three behaviours: a) exploration (number of feeders used during the foraging visit), b) risk avoidance (latency to start feeding) and c) arousal (amount of movements during the foraging visit) in conditions of two different levels of perceived risk (low – control, and high – experimental, with a threatening bullet ant model). Foraging efficiency decreased in response to threatening conditions. However, behavioural traits explained additional variation in foraging efficiency in a condition-dependent manner. More exploration was associated with higher foraging efficiency in control conditions, but this was reversed when exposed to a threat. Regardless of conditions, arousal was positively associated with foraging efficiency while risk-avoidance was negatively related. Importantly, exploratory behaviour and risk-avoidance were quite repeatable behaviours suggesting that they may be related to intrinsic traits of individuals. Our findings highlight the importance of taking into account additional behavioral dimensions to better understand foraging strategies of individuals.

Keywords: risk allocation hypothesis; risk-avoidance; exploratory behaviour; arousal; repeatability

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1. Introduction

A variety of ecological factors has been identified as major determinants in shaping animal's foraging strategies (i.e. resource exploitation). Of those the most commonly evoked are the amount and distribution of available food resources (Morrison et al. 1990; Herborn et al. 2014) and animal motivation (both in the sense of marginal value theorem (Charnov 1976) and/or body condition (Bautista et al. 2001)), but predation pressure is also frequently considered (Lima and Bednekoff 1999). The intensity of a prey vigilance increases with the level of risk predation (probability of predator presence) affecting its foraging efficiency. As the risk allocation hypothesis imposes, a prey allocates time for foraging inversely proportionately to predation pressure (Lima and Bednekoff 1999; Verdolin 2006). Thus, in a given food resources–predation landscape, a fixed foraging strategy is expected to evolve (Krebs 1980). However, increasing number of studies demonstrates a high variation in foraging strategies (Patrick et al. 2014; Cam-

prasse et al. 2017; Moldoff and Westneat 2017), which is hard to explain using only food- and predation-based arguments (Bautista et al. 2001).

Variation in foraging strategies of individuals remains an intriguing topic (Nussey et al. 2007; Bell et al. 2009; Dingemanse et al. 2009; Herborn et al. 2014; Alonzo 2015; Toscano et al. 2016). Existing evidence demonstrates not only the variation *per se* but consistent inter-individual differences in the average level of a behaviour displayed across a range of contexts (Carere and Maestripieri 2013) and in response to environmental variation (Nussey et al. 2007; Dingemanse et al. 2009). Within a species/population, individuals usually represent a full continuum of a given behavioural display, with two polar-opposite phenotypes (e.g. high and low exploratory behaviour) and various intermediate forms in between. Importantly, fitness advantages of contrasting behaviours may differ in various contexts, sometimes dramatically (Smith and Blumstein 2008). For example, highly exploratory behaviour can be advantageous in conditions of resource competition but disadvantageous in a higher predation pressure environment (Dall et al. 2004; Réale et al. 2007; Smith and Blumstein 2008; Quinn et al. 2012b). Despite growing number of studies showing both directly and indirectly behavioural variability in the performance of various strategies, it is still not entirely recognized what could be fitness consequences of variation in these additional dimensions of behavior in foraging performance.

The fitness payoffs of a behavior is likely to be a main source of the observed variation in foraging strategy (Dingemanse and Réale 2005; Smith and Blumstein 2008; Moldoff and Westneat 2017). Under variable conditions, a diversity of behavioral strategies can be maintained if different performance results in different cost and benefits in different contexts. If so, performance may vary as a function of the interactions between social and/or ecological selective forces, which can help reveal the complex interplay of intrinsic and extrinsic factors shaping behavioral variability (Bergeron et al. 2013; Le Cœur et al. 2015; Mouchet et al. 2021; Roth et al. 2021).

Here, we examined the fitness consequences of various behavioural strategies during foraging in wild ranging, Long-billed Hermit hummingbirds (LBHs, *Phaethornis longirostris*). Hummingbirds are known for their extreme metabolism with a high need for energy intake that makes them constantly motivated to forage (Suarez 1992). As such, they are expected to be under strong selection for maximizing foraging efficiency which can have an important effect on fitness. This is particularly significant for trap-lining foraging species, which use flowers, dispersed across the habitat in a route-like fashion (Stiles and Wolf 1979; Araya-Salas et al. 2018). Free ranging foraging entails a period of high vulnerability, exploited by a wide range of predators (Stiles 1978; Owen and Cokendolpher 2006; Lorenz 2007; Zenzal et al. 2013; Sazima 2015; Nyffeler et al. 2017), which in turn, results in a trade-off between efficient foraging and risk avoidance. The differential payoffs in the selective landscape given by these two factors are expected to shape foraging strategies of the hummingbirds.

We assessed the payoffs of different behavioral strategies under a trade-off between food resource exploitation and risk avoidance in Long-billed Hermits. We considered the issue in the context of low and high level of perceived threat and in regard to three behavioural axes, commonly linked to the exploitation of food resources: a) exploration (number of foraging spots (i.e. feeders) used during the foraging visit), b) risk-avoidance (latency to approach the foraging spot to forage), and c) arousal (amount of movements during the foraging event) (Réale et al. 2007; Smith and Blumstein 2008; Couchoux and Cresswell 2012; Quinn et al. 2012a; Herborn et al. 2014). Firstly, we hypothesized that foraging efficiency (expressed here as the amount of time spend on feeding in respect to the total time of the visit at the feeder), may be lower at threatening conditions. Then we hypothesized that foraging efficiency is further modulated by the three behavioural traits (exploration, risk-avoidance and arousal).

2. Methods

2.1. Study species

2.1 would fit better within the introduction

The Long-billed Hermit is a relatively large size hummingbird species of humid neo-tropical lowlands. The species exhibits a lekking mating system in which males sing and display from traditional areas inside the forest for mate attraction, during ca 8 months lasting breeding season (Stiles & Wolf 1979). Unlike many hummingbirds, hermits do not defend a patch of flowers but visit widely scattered flowers in a foraging route (i.e. trap-lining). Aggressive interactions related to disputes over lek territories are common (Araya-Salas et al. 2018). Floaters can be found singing from perches of territorial males while the latter are absent foraging. Territorial ownership is typically regained after an aggressive interaction with intruders, suggesting a selective pressure to reduce foraging time and increase territory attendance. Indeed, more efficient foraging males are more likely to own a lek territory (Araya-Salas et al. 2018).

2.2. Fieldwork

We carried out the study at La Selva Biological Station, Costa Rica (10°23' N, 84°10' W) between May and June 2015. First, to follow behaviour of focal individuals, we captured and individually marked 21 individuals with foam tags (total weight of 0.02 g, which is ~0.3 % of LBH body mass, 6g) with unique colour combinations, attached to the bird back and chest with nontoxic eyelash glue (Araya-Salas et al. 2018). Then, to evaluate foraging efficiency of the marked individuals and quantify it in low and high threat context, we applied a field experiment using a set-up of hummingbird feeders. Commercial feeders (Perky model Pet #209B, 900 ml) were used and modified to have a single opening for accessing "nectar". Three feeders were arranged in a line (separated by ca 10 cm distance from each other, Fig. 1) and filled with a fresh nectar (~30% sugar-water). The set-up was located in a distance of ca 100 m from the lek border. The feeders (filled with nectar filled/changed daily) were exposed in the field for two weeks before the onset of proper experiment, to habituate birds to the study design and feeders location. Location of the feeders did not overlap with foraging area of all the captured individuals, however, as in total we had 12 visitors at the feeders area, while all marked birds were observed on the lek after being caught, either defending territory or as floaters (i.e. all of them survived the capturing and marking procedure and behaved normally at the lek area).

long sentence

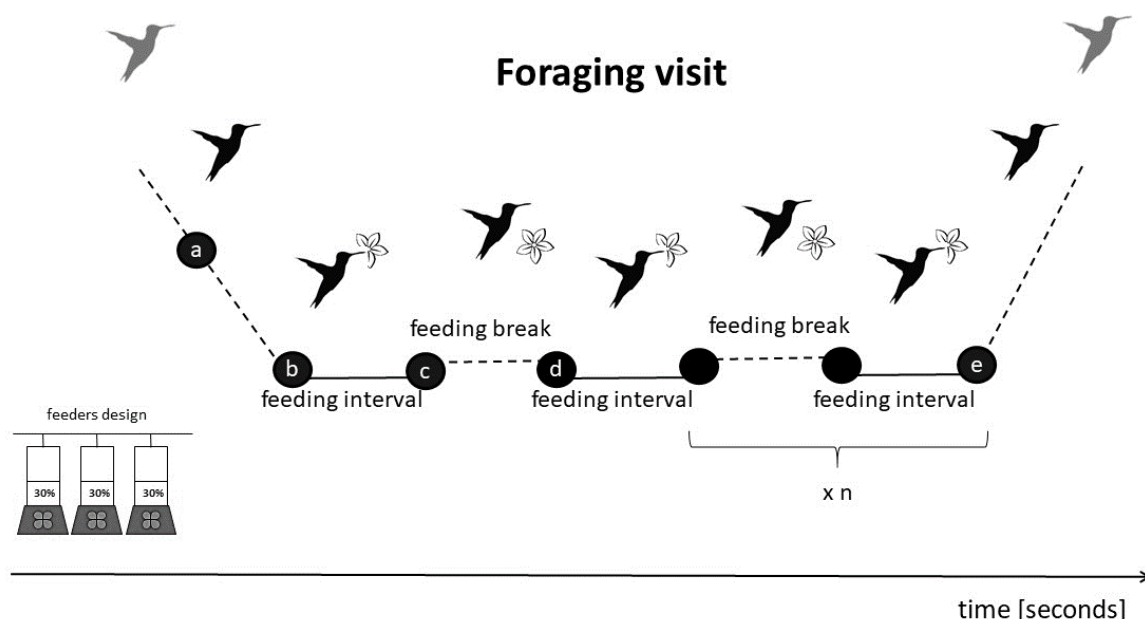


Figure 1. Scheme of the foraging visit – the total time spent by focal bird at the feeders area with at last one feeding event. Time-points crucial for the data analysis denoted with black circles and labelled with letters to denote particular events, being components of the foraging visit: **a)** onset of the foraging visit (appearance in the feeder area, usually hovering in front of the feeder); **b) and d)** onsets of consecutive feeding events (i.e. inserting the bill into the flower-hole of the feeder); **c)** end of the feeding event (i.e. removal of the bill from the flower-hole of the feeder); **e)** end of the foraging visit (i.e. the end of the very last feeding event during the foraging visit). Multiple feedings intervals were possible (1–26, mean: 4.9).

nice figure

can you explain the threat contexts further so others could recreate?

The experiment session consisted of two consecutive phases performed on the same day, in the low (first phase, control) and high threat contexts (second phase, experimental). During the whole experiment birds were allowed to forage on the nectar spontaneously and their behaviour was recorded by a commercial camera (continuous recording mode; model: Fujifilm HS30); camera set up on a tripod in a distance of ca 10 m from the feeders (zoomed on the feeders area). During the second phase, we glued a dead bullet ant (*Paraponera clavata*; found dead in the forest) to each of the three feeders, to simulate a threat. Although the ant is not a predator of hummingbirds, presence of large insects on flowers often scares various hummingbird species (e.g. Carr and Golinski 2020), including Long-billed Hermits (MAS., pers. obs, SOM videos 1 and 2). Importantly, attached bullet ants did not completely scare birds off, allowing the quantification of their foraging behaviour in these circumstances. Hence attaching the bullet ant to the feeders was expected to resemble situations of increased risk of being injured while still exploiting the feeding resource.

We performed three complete experiment sessions (with two phases) and two incomplete sessions (with control phase only, due to weather conditions), all within two weeks (with 2–3 days between sessions). The two complete (two phases) and two incomplete sessions (control phase only) were conducted in the mornings when the foraging activity peak occurs (Stiles & Wolf, 1979), and only a single complete experiment session was performed during an afternoon, when the activity is lower. Since the time of the day, which we considered in the present study, did not affect foraging efficiency considerably (generalized mixed effect model: foraging efficiency ~ hour (fixed effect; numeric) + birdID (random effect); estimate: $-0.009 \pm \text{SE } 0.005$, $t = -1.74$, $df = 137.97$, $P = 0.08$), we did not consider it in further analyses. Besides, since the whole experiment session was

completed within relatively short window of time (up to three hours), we believe that potential day effect should not bias comparisons of the control and experimental phases.

The duration of control phases, including those from incomplete sessions, varied from 0.5 to 3 hours. Owing to regular visits of birds in these control conditions (ranging from 1 to 12 per hour per individual), we could record multiple visits of focal individuals, on average of 6 visits per individual (range 2–18). For experimental phases, we kept recording until all visitors observed during the preceding control phase returned to the feeders, resulting in an average of 3 visits per individual during this phase (range: 1–7). The control phase was performed always before the experimental one as doing so we could ensure recruitment of individuals to both phases. The presence of the bullet ant on their very first encounter with the feeders in a given day might preclude birds to explore the resource. To mitigate the potentially negative effect of bullet ant exposure on the frequency of visits, we performed the sessions with 2–3 days gap in between. For all these practical reasons, we could not randomize treatments and controls phases. The fixed sequence of the experiment phases could bias results on foraging efficiency if that would decrease over the time of experiment session (e.g. due to satiation effect over the whole experiment duration). To address this concern, we analysed foraging efficiency over the consecutive visits using data from control phases (see Supplementary Online Materials, SOM). We found that although foraging efficiency may change over the time that apparently happens only after a considerable number of visits of an individual. Since in our data set it was only the issue with single individuals at single control phases, we considered that issue of not particular importance. Besides, foraging efficiency improved over the time, and given the fact that experiments with bullet ants were always performed after the control phases, if the fixed sequence of the phases biased the results, we would observe an increase or no difference, instead of decrease in foraging efficiency. Since that did not happen, the results of the experiment are apparently solid (SOM, Fig. S1 and S2). Consequently, we treated all the visits of particular individuals as independent data points but obviously controlling for their identity in further analyses.

this belongs in results/discussion/limitations not methods

2.3. Videos analysis

We screened the video recordings with VLC software (www.videolan.org), to locate and cut out video fragments with foraging visits of focal birds. Events of two or more individuals (Long-billed Hermits or a different species) visiting the feeders at the same time were uncommon and were excluded from analysis as interactions disrupted their regular foraging behaviour. A foraging visit was considered whenever a bird inserted the bill into a feeder at least once. For each bird's visit we established key time-points (white and black circles on Fig. 1), with 0.1 seconds precision, using Cowlog software (Pastell 2016). Based on these time-points we calculated the duration of latency to forage, defined as the interval between appearance in the feeder area (when started to hover in front of the feeder in a distance of ca 0.5 m) and the onset of foraging (time from *a* to *b* on Fig. 1); duration of feeding interval/s (time from *b* to *c* on Fig. 1; on average 4.9 events, with a range of 1–26); duration of feeding break/s (time from *c* to *d* on Fig. 1); duration of total foraging (time from *b* to *e*, Fig. 1) and duration of total foraging visit (time from *a* to *e* on Fig. 1). For each visit we also noted which and how many times each of the three feeders were used by the focal bird.

To quantify bird movements around the feeders, we took advantage of the line-arrangement of the feeders that greatly restricted birds activity into two axis. That simplified further analyses, as operating in two-dimensional space we could establish Cartesian coordinates of a bird position for each video frame using the software Tracker version 5.1.5 (physlets.org/tracker). Based on those coordinates we calculated distances between each two bird's positions using Pythagorean theorem.

2.4. Parameters

We calculated foraging efficiency as the ratio of the total duration of foraging (sum of the duration of all feeding intervals) to the total duration of the foraging visit. To characterize foraging strategies we measured three behavioural features that have been linked to intrinsic individual characteristics in other species and shown to affect foraging: exploration, risk-avoidance and arousal (Réale et al. 2007; Smith and Blumstein 2008; Couchoux and Cresswell 2012; Quinn et al. 2012a; Herborn et al. 2014). As a proxy for **exploration** we utilized the rate of visited feeder; the number of feeders divided by the total duration of the visit as visits to new feeders are likely to be a function of time spend at the feeders. As a proxy for **risk-avoidance** we used latency to start to forage, as defined above (time from *a* to *b* on Fig. 1). For both parameters, the higher the value, the stronger was the exhibited behaviour. As **arousal** we considered the coefficient of variance in spatial distances covered by an individual during the whole foraging visit, divided by the number of visited feeders. Therefore, it represents the mean distance covered while visiting a feeder. Higher distances were related to the higher arousal.

2.5. Data analysis

All the analyses were performed in R (R Core Team 2019). Since all parameters had skewed distribution, we log-transformed them prior to analyses (SOM, Fig. S2). To examine how consistent birds are in their behaviour during the foraging, we estimated the repeatability of foraging efficiency, exploration, risk-avoidance, and arousal using *rptR* package (Stoffel et al. 2017). For that we used behavioural features measured during the low risk (control) treatment only, which represented undisturbed conditions and for which we recorded multiple visits per individual. While fitting the repeatability model, we considered given behavioural variable (response variable) and birds identity [explanatory variable/random effect] (Stoffel et al. 2017).

To assessed variation in foraging efficiency (response variable) as a function of threat level and intrinsic behavioural features (exploration, latency and arousal as predictors) we applied a Bayesian generalized linear mixed model with individuals as a random effect. We fitted three models representing alternative hypotheses explaining variation in foraging efficiency. The first model represents a more traditional view of foraging behaviour in which efficiency is only affected by the level of threat. The second model included an interaction among behavioural traits and threat level, which represents a more nuanced scenario in which the interplay between threat level and intrinsic behavioural differences determines foraging efficiency. There was only little collinearity between predictors (correlation coefficient range from -0.21 to -0.10; SOM, Fig. S3). We run this model with a single predictor for intrinsic behavioural trait (separately considering arousal, exploration and risk-avoidance) as well as in a form of a global model, with all behavioural predictors included. The two approaches yield qualitatively similar results, therefore we presented here only the outcome of the global model. while the outcome of the single behaviour-predictor models are presented in SOM, Table S1, Table S2, Fig. S4). Finally, we fitted an intercept-only model representing the scenario in which the proposed predictors do not affect efficiency. All the three alternative models were compared using model selection based on the deviance information criteria (DIC) (Meyer 2016). Models were fitted using the R package *MCMCglmm* (Hadfield 2010).

Please add details of ethical approval to Methods section

3. Results

Repeatability of all the parameters was moderate but significant for all the parameters except for arousal (Fig. 2). When predicting foraging efficiency, the model including all intrinsic behavioural traits and their interaction with the risk predation context performed significantly better than a simpler model including only threat context (Table 1). All parameters and their interaction were significant in this model except for risk-avoidance (Table 2). Overall, foraging efficiency was lowered in the higher threat context (Fig. 3) and the effect of behavioural parameters on the foraging efficiency was context

dependent (Table 2). The most dramatic effect was found in respect to exploratory behaviour, which was positively related to foraging efficiency in low threat context but the opposite pattern was observed in the higher threat context (Fig. 4). Arousal was positively related to foraging efficiency and this was particularly pronounced when birds faced higher threat (Fig. 4). Risk avoidance overall tended to decrease foraging efficiency but that was not significant and did not differ between threat levels (Fig. 4).

Table 1. Ranking of models explaining foraging efficiency of Long-billed Hermits, ordered by delta Deviance Information Criterion (DIC; Akaike's Information Criterion AIC yields to same conclusions).

Predictors	df	DIC	Δ DIC	weight DIC	AIC	Δ AIC	weight AIC
md_all_interactions	10	-400.0909	0.00	1	-396.3073	0.00	0.99
md_arousal_exploration	8	-388.2385	11.85	0	-386.2831	10.02	0.01
md_arousal_risk_avoidance	8	-378.9807	21.11	0	-376.8184	19.49	0.00
md_arousal	6	-363.3410	36.75	0	-363.2509	33.06	0.00
md_risk_avoidance_exploration	8	-350.1568	49.93	0	-348.8140	47.49	0.00
md_exploration	6	-345.7716	54.32	0	-346.4065	49.90	0.00
md_risk_avoidance	6	-315.2258	84.87	0	-315.0929	81.21	0.00
md_context	4	-308.6036	91.49	0	-310.7995	85.51	0.00
md_null	3	-296.3098	103.78	0	-299.8347	96.47	0.00

Table 2. Effects of behavioural variables and experimental context (low/high risk) on foraging efficiency of Long-billed Hermits (N individuals = 12, N data points = 192). Common intercept = 0.4548, effects are slope estimates derived from the first top Bayesian MCMC generalized linear model (Table 1). Significant effects denoted in bold.

Predictor	Effect size	CI 2.5%	CI 97.5%	pMCMC
contextHigh risk	-0.1409	-0.2732	-0.0132	0.0322
arousal	0.0684	0.0275	0.1083	0.0006
exploration	0.3686	0.1244	0.6167	0.0023
risk_avoidance	-0.0327	-0.0663	0.0023	0.0641
contextHigh risk:arousal	0.2445	0.1541	0.3436	0.0001
contextHigh risk:exploration	-0.8355	-1.1641	-0.4925	0.0001
contextHigh risk:risk_avoidance	-0.0270	-0.0793	0.021	0.2918

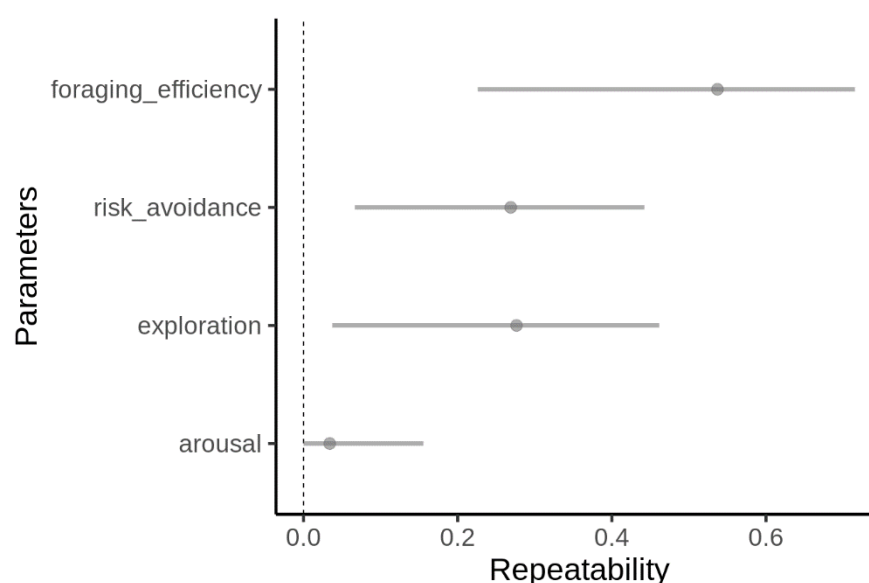


Figure 2. Repeatability estimates of foraging efficiency and behavioural parameters in the Long-billed Hermit measured with linear mixed-effects models (Nakagawa and Schielzeth 2010). 278
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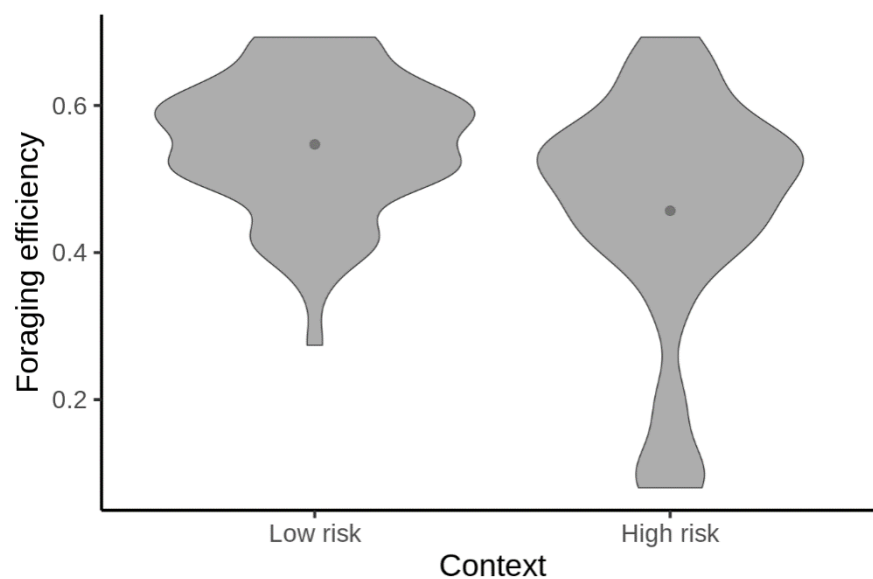


Figure 3. Foraging efficiency in the context of low and high levels of perceived risk of predation. 280
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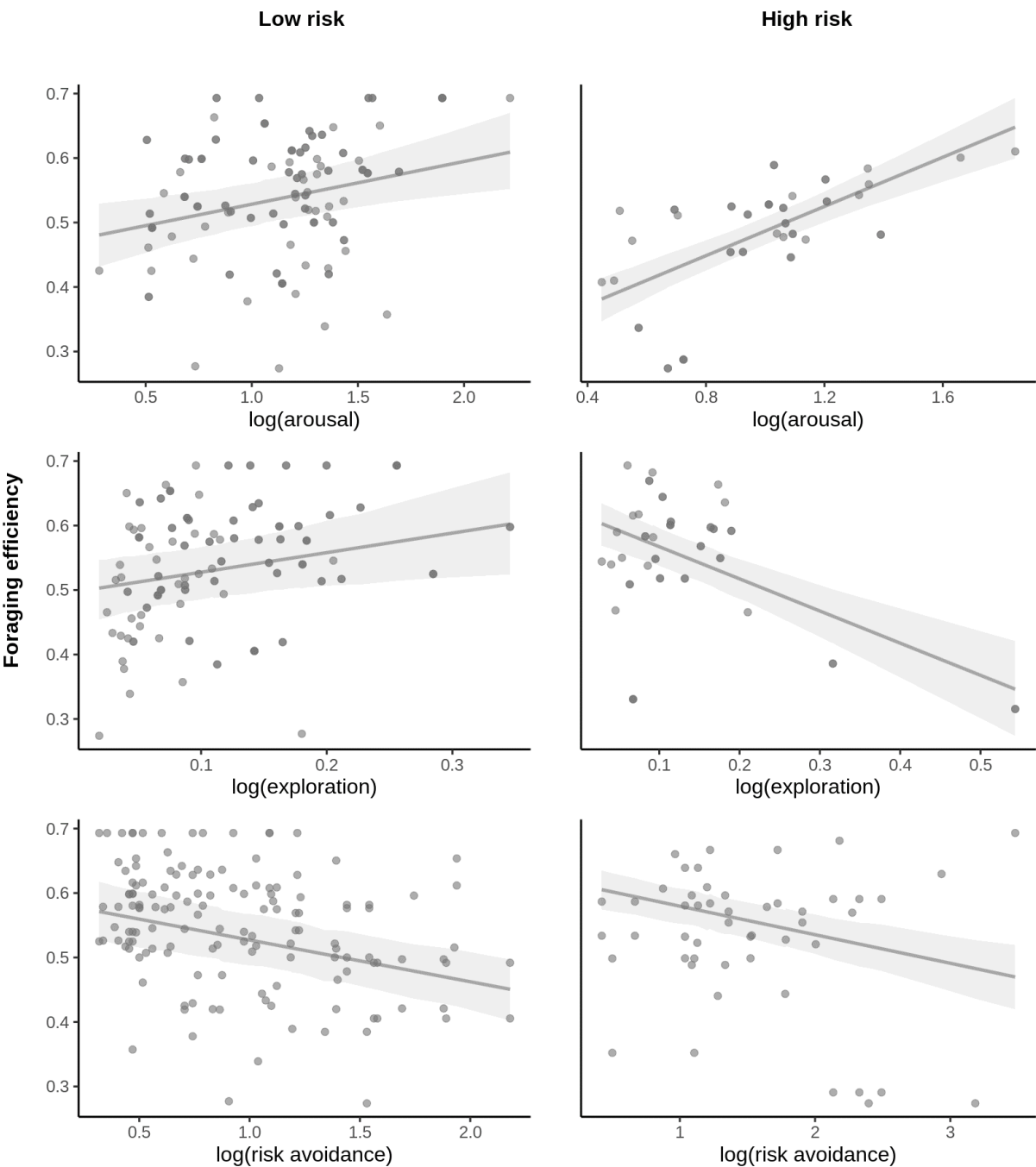


Figure 4. Foraging efficiency of Long-billed Hermits in regard to their behavioural performance (exploration, risk avoidance and arousal) in the context of low and high levels of perceived risk of predation.

4. Discussion

As we could expect under the risk allocation hypothesis (Lima and Bednekoff 1999) foraging efficiency of Long-billed Hermits decreased in response to threatening conditions. However, behavioural performance in regard to exploration, risk-avoidance and arousal additionally affected the foraging efficiency, interestingly, in a condition-dependent manner. These results suggest that a range of strategies instead of a single fixed strategy should be considered, when modelling foraging behaviour in a threaten-

ing context. The results also highlight the importance of behavioural variability in shaping evolution of foraging strategy.

Despite not being a specific prey target, hummingbirds may be opportunistically hunted by a wide range of predators (e.g. Owen and Cokendolpher 2006; Lorenz 2007; Zenzal et al. 2013; Sazima 2015; Nyffeler et al. 2017). That imposes a considerable predation risk and favours evolution of risk-avoidance behaviour. Indeed, we found that experimental exposure of an ant, potentially representing just a threat of being bitten (but not eaten), was enough for LBHs to exhibit some behavioural changes. Importantly, despite of the threat, birds did forage although with a lower efficiency. This places LBHs in a group of species representing so call paradox of risk-allocation hypothesis - in conditions of a frequent predator presence, prey might need to forage actively even though a threat (either potential or real predator) is present (Lima and Bednekoff 1999; Ferrari et al. 2009). It is worth to evoke in that context one of assumptions of the risk allocation hypothesis, which is 'living on the edge' in terms of meeting energy demands (Lima and Bednekoff 1999; Verdolin 2006). This assumption seems to be rarely met in most of animal species used to test the hypothesis so far ((Ferrari et al. 2009)). Hummingbirds, given their extreme metabolism rate, could be a rare example when the assumption is actually true.

In control conditions individuals exhibiting more exploratory behaviour had also overall higher efficiency during the foraging visit. Reversed pattern was observed for the experimental conditions. A simple reason of the reversed pattern could be that each time an individual stopped feeding to change a feeder it had longer time intervals, probably associated with the need to analyse "*de novo*" the risk situation. The fact, that individuals were consistent over the time and context in their exploration suggests that this behaviour may be related to personality (Dingemanse and Réale 2005; Réale et al. 2007; Dingemanse et al. 2010; Montiglio et al. 2015). If indeed the exploratory behaviour examined here is a personality trait, and that trait has different fitness consequences in regard to predation, the predation pressure is likely to shape distribution of exploration phenotypes in the population. Although we are not able to test this prediction currently, to encourage future studies, we highlight the role of predators in the evolution of personality (Dingemanse and Réale 2005; Exnerová et al. 2010; Nácarová et al. 2018).

There was a clear tendency that risk-avoidance behaviour negatively affects foraging efficiency. In the global model we present in the main text it was not significant, but when a single trait model was considered the effect was apparent (Table S2, SOM). That indicates that in the most extreme scenario individuals exhibiting high risk-aversion might jeopardize their survival in terms of energy intake while individuals with low-risk aversion, although benefiting from high foraging efficiency, would be more likely to be predated. If the risk-avoidance was related to birds personality, the relationship between that and foraging efficiency would contribute in the selection of given behavioural phenotype in given predation risk level. Consistently, frequent changes and/or unpredictable level of risk predation in the environment would maintain variability in this behavioural phenotype (Smith and Blumstein 2008).

To maximize fitness, hummingbirds should adaptively allocate both the exploratory and risk-avoidance behaviours. Here we considered the issue in respect to a given species but interpreting our study we could speculate that these two behaviours were also differently allocated in hummingbirds that differ in foraging strategy, trapliners and territorials. The two groups are likely to experience different predation level, and so others behaviours like exploration and risk-avoidance could also differ. All that might then affect foraging performance (Gill 1988; Ohashi and Thomson 2005; Tello-Ramos et al. 2015). Thus, our study suggest possible importance of predator pressure in shaping foraging strategy of various hummingbirds.

An increasing foraging efficiency with an increase in arousal may be counterintuitive at first glance, time allocated to movements potentially limits the time for foraging.

However, arousal was not a repeatable trait, thus an animal arousal may be an outcome of its nutritional state. Then more active individuals could be more effective during the foraging, owing to their good body condition or high motivation to forage.

Both exploratory and risk-avoidance behaviour were quite repeatable for individuals suggesting that these two behaviours are potentially related to birds personality (Sih et al. 2004; Dingemanse and Réale 2005; Cleasby et al. 2015). In a constantly changing environment, varying fitness consequences of given behavioural phenotype would maintain variation in animals personality (Smith and Blumstein 2008). If indeed the exploratory and risk-avoidance behaviour are at least partially heritable personality traits, one could use them to model an evolutionary scenario for given behavioural phenotypes in various conditions of predation pressure. We are currently not able to perform any analysis of that kind given the relatively low number of tested individuals but we point out hummingbirds as potential animal model species in the studies of animals personality.

Include limitations of the study in discussion and suggestions for future research.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, **Figure S1.** Relationship between foraging efficiency and consecutive visits at feeders area during the control phases of the experiment (all individuals considered); **Figure S2.** Autocorrelation analysis plots for six time series (four individuals) of foraging efficiency during consecutive visits at feeders area during the control phases of the experiment. The titles denote individual identity and number of control session. Solid vertical lines denote correlation coefficient for particular lag of the time series, and dashed horizontal lines delimit the range of their significance; **Figure S3.** Distribution of foraging efficiency and behavioural parameters in the study population of the long-billed hermits, raw (A) and log-transformed (B) data; **Figure S4.** Correlation coefficients between the three behavioural variables; **Figure S5.** Comparison of estimates from single predictor models and the global model; **Table S1.** Ranking of models explaining foraging efficiency of Long-billed Hermits, ordered by delta Deviance Information Criterion (DIC; Akaike's Information Criterion AIC yields to same conclusions). Best model for each parameters is bolded; **Table S2.** Effects of behavioural variables and predation context on foraging efficiency of long-billed hermits. Effects are model slope estimates derived from Bayesian MCMC generalized linear model. Only models that improved fit compared to the null models are presented.

Author Contributions: Authors equally conceived the study, contributed to data collection, data analysis and manuscript writing.

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Institutional Review Board Statement: All activities (birds marking, feeding, and video recording/observations) were performed with the greatest care. The capturing and marking procedure did not have apparent effect on birds survival, as all the individuals where observed in the lek and/or at the feeders area after the capturing. The foam with with the birds were marked was of negligible weight (0.02 g, which constitutes ~0.3% of average body mass (6g) of LBH). The study was reviewed and authorized by the Costa Rican Ministerio del Ambiente y Energia (063-2011-SINAC), and performed in accordance with their guidelines and regulations.

Data Availability Statement: Data associated with the manuscript included as supplementary materials.

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Conflicts of Interest: Authors declare not conflict of interest.

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