Intrabrood rank, age, and adult presence predict novelty-seeking in individual Arabian Babblers (*Turdoides squamiceps*)

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1 Risk taking and neophilia affect many aspects of an individual's life trajectories including social
2 rank, philopatry, reproductive success, and mortality. We investigate mechanisms by which early
3 life socialization may have lasting impacts on behaviours across contexts by assessing the
4 relationship between social rank and neophilia at different stages of development. In the
5 cooperatively breeding Arabian babbler (*Turdoides squamiceps*) age is positively correlated with
6 dominance and reproductive skew. Early life socialization, here represented by social rank order
7 relationship to clutch mates may provide a major additional source of variation within age
8 cohorts in overall social opportunities and the resulting reproductive strategies. We test the
9 hypothesis that novelty-seeking behaviour is related to intrabrood rank in Arabian babblers; we
10 presented familiar or novel, and stationary or moving objects, and familiar or novel sounds, to
11 birds. To examine intrabrood dominance as a potential predictor of later-life neophilic behaviors,
12 a multimodal index of novel stimulus-approach behaviour was constructed for fledglings and
13 juveniles living in an individually marked population, and compared against an intrabrood rank
14 metric based on scramble competitions (rank index), generated to allow comparisons between
15 different broods and groups. All birds were more likely to react to novel than to familiar stimuli.
16 Intrabrood rank index positively predicted the frequency of novel stimulus approach, with
17 individuals of higher intrabrood rank more frequently approaching novel stimuli. Juveniles made
18 more approaches to novel stimuli, and made those approaches earlier in the trial, than did
19 fledglings; approaches by all young birds were more frequent when an adult was present at the
20 beginning of the presentation. These findings suggest an interaction between novelty-seeking
21 behaviour by young birds and displays related to social rank and/or competitive ability. In this
22 way, novelty-seeking behaviours in early life may be connected with lifetime social and
23 reproductive trajectory.

Keywords: Neophilia, Risk-taking, Social rank, Ontogeny.

Risk taking and neophilic behaviour, plastic or chronic, play important roles in reproductive opportunities and the resulting impact on lifetime fitness (Boissy, 1995; Smith & Blumstein, 2008). Among birds, intraspecific variation in neophilic behaviour has been linked with ecological plasticity, learning speed, and innovation (Greenberg & Mettke-Hofmann, 2001). Self-exposure to novel stimuli is by definition a gamble, and constitutes a strategic choice (Boissy, 1995; Greenberg & Mettke-Hofmann, 2001). Neophilic behaviour can be a facultative strategy when resources fluctuate, to permit information gathering (Greenberg & Mettke-Hofmann, 2001), and has been linked to social rank and experiential outcomes of social conflict in a wide variety of taxa including fish (e.g. Frost, Winrow-Giffen, Ashley & Sneddon, 2007), birds (e.g. Stöwe et al., 2006; David, Auclair & Cézilly, 2011), and mammals (Chamove, 1983).

The direction of the relationship between novel stimulus approach and social rank is not uniform among birds, or even within species (Dingemanse & de Goede, 2004; Boogert, Reader & Laland, 2006; Stöwe et al., 2006; David et al., 2011). Neophilic behaviour is shown to be positively and negatively associated with social dominance, dependent on ecological and social context (Greenberg & Mettke-Hofmann, 2001; Dingemanse & de Goede, 2004; Stöwe et al., 2006). Among zebra finches (*Taeniopygia guttata*), neophobia has a strong negative relationship with social dominance (David et al., 2011). Adult male great tits (*Parus major*) with established territories, and which are quicker to explore a new territory, are also more socially dominant (Dingemanse & de Goede, 2004). In turn, amongst younger male great tits without established territories subordinate individuals are quicker to explore (Dingemanse & de Goede, 2004). Finally, when exposed to novel objects in pairs, the subordinate member of male-male dyads of ravens (*Corvus corax*) would approach first, while in mixed sex dyads dominants approached

first (Stöwe et al., 2006), but Stöwe and Kotrschal (2007) also found no effect of social rank on novel object approach in ravens.

It has been suggested that subordinate individuals are more likely to take risks in foraging, driven by lower resource access than dominant individuals (Bergmüller & Taborsky, 2010). In this theory, socially subordinate individuals should have lower latency to approach novel objects, as dominant individuals are capable of monopolizing the resource even if they approach later (Boogert et al., 2006). Alternatively, if novel objects are inherently appealing, or if subordinates experience social inhibition in the presence of dominants (Stöwe et al., 2006), socially dominant individuals will monopolize novel resources.

The Arabian babbler *Turdoides squamiceps* is a cooperatively breeding bird which lives in highly exclusive social groups with a fixed hierarchy (Zahavi, 1990; Kalishov, Zahavi & Zahavi, 2005). Age appears to be strongly and positively correlated with social dominance and reproductive skew in babbler groups (Zahavi, 1990), making the competitive relationships among brood mates and group composition during early life a major potential source of individual variation in social experience and strategy, including succession to social dominance. Within clutches (age cohorts), the apparent social dominance structure is the result of competition in the first few weeks of life (Zahavi 1990). Food division among nestlings, which may influence competitive ability, appears to be determined (cyclically) by clutch mate competition rather than hatch order, though if older individuals are experimentally cross-fostered, they appear to have greater competitive ability (Ostreiher 1997). We investigate the role of ontogeny by focusing on early life predictive effects of intrabrood rank on novel stimulus approach in this cooperative breeding species (Bergmüller & Taborsky, 2010).

Social facilitation of novel object investigation may or may not depend on prior experiences; for example, observing the interaction of a conspecific with an uncertain or potentially risky stimulus can be a useful form of risk-avoidance (Griffin & Boyce, 2009). In turn, the quality or nature of a new food item, or new mechanism for acquiring a food item, can also be socially transmitted (Langen, 1996; Fritz & Kotrschal, 1999). Individual differences in producer/scrounger tactics and innovation in foraging strategy have been associated with adult breeding rank in Arabian babblers: adult subordinates (nonbreeders) are more likely to observe the location of food by dominants than to find food themselves (acting as scroungers) and faster to innovate foraging strategies than dominants (Keynan, Ridley & Lotem, 2014). An important influence on the behaviour of young individuals is the observation of adult behaviour. We therefore also examine the relationship between adult presence and investigation of novel stimuli by young.

Our research is aimed to distinguish between two main hypotheses: that the social rank of individuals influences the likelihood of those individuals either to avoid stimuli of uncertain risk value or to seek them. In the risk-averse hypothesis, novel stimuli are potentially threatening, and subordinates will approach more frequently and/or more quickly than dominants, which have greater access to food and other resources (resource access) and do not need to take such a risk (Laland & Reader, 1999; Thompson et al., 2013). In the risk-seeking hypothesis, individuals are attracted to novel stimuli as potentially valuable resources worth monopolizing. Monopolization of items of uncertain value, or repeated approach, may also be a result of a winner effect (Frost et al., 2007), or an honest signal of ability. In this model dominant individuals will approach more frequently and/or more quickly than will subordinates, as an extension of the greater resource access exercised by dominants. We set out to address the way in which early life intrabrood

social rank – a measure of early life sibling social relationship - may relate to the perceived risk or reward value of novel object approach; an inherent gamble.

To comprehensively assess approach to different types of novelty, we present both stationary and moving objects as well as acoustic stimuli to babbler groups. Each stimulus modality had a familiar and a novel stimulus type. The order of presentation was included as a potential confound in our models. Our statistical models also accounted for potential effects or confounds of a variety of individual traits, sex ratio, sex, age class (fledgling/juvenile), and group size on the frequency and latency to approach novel stimuli.

METHODS:

Subjects:

19 juvenile (defined as 3-11 months old) Arabian babblers (average age: 163 days, ranging from 93-246 days) from six groups and 13 fledglings (defined as up to 3 months old) (average age: 26 days, ranging from 15-34 days) from four groups of free-living Arabian babblers were included in the study. Due to cases of disappearance/mortality before the age of conspicuous sexual dimorphism, the sexes of some birds remain unknown. All individuals in the study occupied mixed-sex groups at the time of the trials. The birds were studied in the Shezaf Nature Reserve in the Negev Desert near Hazeva, Israel. The population has been the focus of an ongoing study organized and maintained by Professors Amotz and Avishag Zahavi (e.g. Zahavi, 1990) and their research group for 40+ years. All birds are habituated, banded, and censused on a regular basis. Banding of nestlings occurs at approximately eight days of age. Habituation includes presentation of food items (mealworms and/or bread) to individuals on a regular basis.

114 *Data Collection:*

115 *Intrabrood rank testing:*

116 *Paired Scramble Competitions:*

117 To establish intrabrood ranks, the standard operating protocol involves the presentation of live
118 mealworms (one mealworm per test), obtained from Tel Aviv University, when young (<5
119 months) were approximately equidistant from and within a meter of seated observer, in an
120 adaptation of the method described in Carlisle and Zahavi (1986). The winner and social
121 aftermath (defined as the next interaction between participants within fifteen seconds) is
122 recorded for each fledgling. A simple dominance index was established to permit comparison of
123 relative social rank among birds of different clutches and groups. The formula utilized was: #
124 wins / # surviving clutchmates. This index was generated for each individual relative only to
125 members of its own clutch, to better separate the effects of intrabrood rank and interbrood rank
126 (age based dominance). Hatch order within clutches was not known.

127

128 *Novel/familiar stimulus approach experiment:*

129 *Presentations:*

130 Each group (and consequently all individuals) was exposed to all stimuli on five different days.
131 During the sessions, all six condition types were presented in a randomized order (random.org)
132 over the space of two hours.

133 The presenter (AGF) walked with birds (< 10 m from at least one individual most of the
134 time) for 15+ minutes before initiating experimental presentations, waiting for birds to resume

normal foraging behaviour. Presentations lasted 1 minute from the beginning of data collection to the end. 10+ minutes (depending on behaviour of birds and proximity to presenter) were allowed to pass between presentations to permit a return to normal foraging state (as subjectively assessed by observer).

When all juveniles or fledglings were within approximately 5 m of one another, and within approximately 10 m of the presenter, stimuli were deployed. Following the initiation of the presentation, the presenter moved slowly away from the stimulus to a distance of 5 m (as calculated by eTrex GPS) from the stimulus. Birds were exposed to stimuli during this period but recording did not begin until the observer was in location. The stimulus and the area (30 cm surrounding it) were observed through binoculars to permit accurate color ring assessment to identify each participating individual bird.

Table 1. Presentation types

Modality	Trial Class	Stimulus	Description
Stationary object	Familiar	Rock	Ovoid. ~ 10 x ~ 6.5 x 3 cm.
Stationary object	Novel	Kitchen sponge	Rectangular. Iridescent blue and silver. 8.25 x 10.8 x 2 cm.

Moving object	Familiar	Leaves (moved with dental floss string)	End of a date palm frond with leaves, found on the reserve. ~17 x 12 cm. POH Dental Floss: “No Wax™ Classic 490
Moving object	Novel	Plastic rectangle (moved with dental floss string)	Yellow. 19 x 11.5 cm. POH Dental Floss: “No Wax™ Classic 490
Acoustic	Familiar	Recording of white spectacted bulbul (<i>Pycnonotus xanthropygos</i>)	30 second playback repeated through trial. These birds coexist with the study population and are relatively common on the reserve.

Acoustic	Novel	Recording of	30 second
		“Pennsylvania	playback repeated
		65000” from the	through trial.
		Glenn Miller	Unfamiliar
		album “Pure	anthropogenic
		Gold”	sound
			arrangement.

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148

149 *Stationary:*

150 Objects were deployed by hand.

151 *Moving:*

152 Objects were deployed by hand, then drawn slowly towards the observer in *ad libitum*
153 trajectories by use of dental floss string tied to the object.

154 *Sound:*

155 Two sounds were played at identical volume settings and peak amplitudes from an iPod 4™
156 connected to an X-Mini II XAM4-B Portable Capsule Speaker™. Both speaker and iPod were
157 covered in cloth and concealed in sand to standardize and mitigate visual interference in the
158 acoustic signal. The sounds were audible to the observer at five meters.

159 Stimuli were removed by the observer after 1 min. Gaps between stimulus presentations lasted
160 10 min. or more.

161

162 *Data Collection:*

163 Data were collected during September-November 2013 and March-May 2014. Observations
164 began when the observer was positioned at five meters distance. No approaches made by birds
165 while the observer was in motion were recorded. A record was made if an adult was standing
166 within ~ 30 cm of the stimulus at the beginning of a given session. Each approach (defined by
167 movement towards the stimulus within ~ 30 cm) by a juvenile or fledgling was recorded.

168

169 *Analysis:*

170 The average latency to first approach was calculated for each bird, along with the average
171 frequency of approach to each stimulus per trial (the number of times an individual came within
172 ~30 cm of the stimulus). A general linear model is presented, in which we used a backward
173 elimination procedure (Grafen & Hails, 2002). We used trial modality (stationary object, moving
174 object, acoustic playback), trial class (familiar/novel), order of presentation (order in which
175 stimuli of each modality/class were presented), adult presence (within 30 cm of the stimulus at
176 the beginning of a session), age class (fledgling/juvenile), group size, individual ID, clutch ID,
177 sex, sex ratio, and intrabrood rank as predictor variables, and frequency and latency as response
178 variables (in separate tests). Sex was excluded from the analysis but included in the lack of fit.
179 Trial modality, individual ID, and clutch ID were random effects. We removed the least
180 significant non-significant predictor from each model, resulting in a reduced model with
181 significant predictors and the predictor of main interest: treatment. This treatment predictor was

retained in model regardless of its significance. The full and the step-wise reduced models are all shown below. Analyses were performed in SAS/JMP 11 statistical software™.

Ethical Note:

Procedures unique to this research, added to the general practices of the Arabian Babbler Project based out of Tel Aviv University (described in Zahavi, 1990), were approved by the IACUC of Hunter College, City University of New York, New York, New York, 10065, protocol number “MH-social 2/18/01 Social ontogeny of the cooperatively breeding Arabian babbler (*Turdoides squamiceps*).” Please see above for life history information of study subjects. No stimuli resembled or simulated predators. Individuals were identified with unique combinations of coloured rings on their legs, each ring ~0.5 cm in width.

RESULTS:

Predictors of latency to first approach:

The full model included all predictors (Table 2a, 2b). The least significant predictor, rank index was then removed. The least significant predictor in the revised model was the order of presentation and also removed. The third fit showed the least significant predictor to be adult presence. The fourth model excluded adult presence. The least significant predictor was age class by trial class. A new model excluded age class by trial class. The least significant predictor in this model was sex ratio, excluded from the subsequent model. The resulting model revealed age class by rank index as the least significant predictor. The new model excluded age class by rank index and showed the least significant predictor to be trial class. A fit excluding trial class

204 showed that group size trended towards significance as a positive predictor of latency to first
 205 approach.

206 The final model retained only age class as a predictor of latency to first approach.
 207 Juveniles were significantly quicker to approach stimuli than fledglings (Fig. 1).

208 **Table 2a. Latency to approach: predictor effects**

209

Fit Model	Least significant predictor	Effect size	SE	df	P	Wald statistic
Full Model	Rank index	-0.164	1.114	1	0.882	
2 nd Model	Order of presentation	-0.129	0.377	1	0.731	
3 rd Model	Adult presence	0.303	0.720	1	0.673	
4 th Model	Age class*Trial class	-0.533	1.080	1	0.621	
5 th Model	Sex ratio	-1.072	1.811	1	0.555	
6 th Model	Age class*Rank index	1.097	0.794	1	0.185	
7 th Model	Trial class	1.172	0.784	1	0.136	
8 th Model	Group size	0.592	0.327	1	0.094	
Minimal Model	Age class	7.601	1.004	1	< 0.0001	7.57

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211 **Table 2b, Latency to approach: fit models**

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Fit Model	Predictor	r^2 adjusted	RMSE	P
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removed to create model				
Full Model	None	0.164	11.864	< 0.0001
2	Rank index	0.166	11.848	< 0.0001
3	Order of presentation	0.168	11.833	< 0.0001
4	Adult presence	0.172	11.814	< 0.0001
5	Age class*Trial class	0.173	11.801	< 0.0001
6	Sex ratio	0.179	11.781	< 0.0001
7	Age class*Rank index	0.178	11.794	< 0.0001
8	Trial class	0.172	11.827	< 0.0001
Minimal Model	Group size	0.171	11.855	< 0.0001

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214

215 **Table 3. Covariance Matrix of Component Estimates: latency to approach**

Random Effect	ID	Clutch	Trial Modality (Stationary, Moving, Acoustic)	Residual
ID	25.176	-11.220	0.183	-7.705
Clutch	-11.220	9.9154	-0.120	0.165
Trial Modality (Stationary, Moving, Acoustic)	0.183	-0.120	1.428	-1.042
Residual	-7.705	0.165	-1.042	123.925

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Figure 1. Mean and + *SE* latency to first approach divided by age class (fledgling/juvenile) and trial class (familiar/novel).

Predictors of approach frequency:

The full fit model included all predictors (Table 4a, 4b). The least significant predictor, group size was removed. The least significant predictor in the revised model was order of presentation. The third fit contained only one nonsignificant predictor: sex ratio. Sex ratio was removed, resulting in the the final model that included rank index, trial class (familiar/novel), adult presence at the beginning of the trial, age class (with the nested predictor: sex), age class by trial class, and age class by rank index. Young Arabian babblers preferentially responded to novel stimuli: novelty (vs familiarity) was a positive predictor of approach frequency (Fig. 2). Intrabrood rank positively predicted frequency of approach (Fig. 3). Juveniles were more likely

to approach stimuli than fledglings (Fig. 2). The presence of an adult at the beginning of a trial increased the frequency of approach (Fig. 4).

Table 4a. Frequency of approach: predictor effects

Fit Model	Least significant predictor	Effect size	SE	df	P	Wald statistic
Full Model	Group size	-0.039	0.023	1	0.117	
2 nd Model	Order of presentation	0.006	0.014	1	0.679	
3 rd Model	Sex ratio	-0.009	0.053	1	0.864	
Minimal Model	Rank index	0.222	0.029	1	< 0.0001	7.44
	Trial class	-0.426	0.047	1	< 0.0001	-13.96
	Adult presence	0.174	0.028	1	< 0.0001	-6.13

Table 4b. Frequency of approach: fit models

Fit Model	Predictor removed to create model	<i>r</i>² adjusted	RMSE	P
Full Model	None	0.542	0.769	0.006
2	Group size	0.543	0.768	0.02
3	Order of presentation	0.544	0.768	0.007

Minimal Model	Sex ratio	0.544	0.767	0.0002
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Table 5. Covariance Matrix of Component Estimates: frequency of approach

Random Effect	ID	Clutch	Trial Modality (Stationary, Moving, Acoustic)	Residual
ID	0.000	0.000	7.638×10^{-8}	-2.482×10^{-5}
Clutch	0.000	0.001	-1.431×10^{-7}	5.413×10^{-8}
Trial Modality (Stationary, Moving, Acoustic)	7.6389×10^{-8}	-1.431×10^{-7}	8.511×10^{-6}	-2.348×10^{-6}
Residual	-2.482×10^{-5}	5.413×10^{-8}	-2.348×10^{-6}	0.000

Figure 2. Mean and + *SE* frequencies of approach separated by age class and trial class. Age class is divided between fledglings and juveniles. Trial class is separated between novel stimulus and familiar stimulus.

Figure 3. Mean frequencies of approach by rank index, separated by age class.

Figure 4. Mean and + *SE* frequency of approach with adult present or absent (in proximity to stimulus: please see methods) at the beginning of the recording session.

DISCUSSION:

We found support for a risk-seeking hypothesis across family groups of Arabian babblers. Latency to first approach of all stimuli was negatively predicted by age, supporting the hypothesis that risk/novelty seeking increases with development/nutritional independence (Fig 1). Trial class predicted approach, with novel objects being approached more frequently (Fig 2). Individuals more socially dominant to their clutch mates were more likely to approach stimuli (Fig 3). Juveniles (average 163 days) were more likely to approach than fledglings (average 26 days) (Figs 2, 4), and the interaction between rank index and age class positively predicted approach frequency. This may be confounded by the age-based hierarchy which has been reported in the species (Zahavi, 1990). Juveniles were not tested at the same time as fledglings,

but age variation within age classes (due to the presence of different clutch cohorts within age classes within some groups) and relative rank within the group due to the presence or absence of older birds may have affected our results. For this reason, further research is necessary to parse apart the relationship between relative age and overall social rank with regard to novel stimulus approach. Juveniles of higher relative dominance over their own clutch mates were the most likely birds to approach stimuli (Fig 2, 3). The presence of an adult at the beginning of recording also positively predicted approach frequency (Fig 4), supporting a scrounger or observational learning context for novelty-seeking behaviours in this species, though as noted below, it is important to acknowledge that fledglings are rarely distant from adults due to nutritional dependence on parental provisioning (e.g. Ridley 2007).

Our results shed light onto a longstanding discussion on the relationship between social rank and neophilia, in which arguments have been made for both positive and negative correlations depending on ecological and social context (Boogert et al., 2006; Greenberg & Mettke-Hofmann, 2011). Unlike tests exploring the relationship through novel foraging behaviours, our study did not pair novel stimuli with food resources (Griffin, Lermite, Perea & Guez, 2013). We found that novel-stimulus approaches in a familiar social context (the natal cooperatively breeding social group) are positively linked to the rank order of resource monopolization in that same context in Arabian babblers, as seen before (Clutton-Brock & Harvey, 1976; Carlisle & Zahavi, 1986). Resource monopolization is fundamentally linked to intrabrood rank in many bird species (Drews, 1993), including in Arabian babblers which compete with siblings for resources by monopolizing space within the nest (Ostrieher, 1999), starting soon after hatching. Expressions and reinforcements of social rank among the juveniles

begin early in life and are often elicited by competition for food encountered during foraging (Carlisle & Zahavi, 1986; Zahavi, 1990).

While the similarity of babbler responses to the different stimulus modalities presented in this study (stationary object, moving object, and acoustic) suggests a generalized response to novelty, greater variation in stimuli presented will further resolve this question. A wider range of objects featuring greater variation in size, color/pattern, movement path, and/or acoustic structure remains necessary to develop a more detailed understanding of the relationship between novel object approach and risk taking. For example, none of the stimuli presented in this study were intended to resemble specifically high risk stimuli (such as predators or dangerous anthropogenic items/sounds found near the habitat including tractors or other machinery). Nor were the objects specifically designed to be associated with sources of food (for example, babblers may actively overturn sections of dried mud, or inspect stationary plant material, during foraging). In this way the neutral aspect of the stimuli permitted us to better access the inherent risk/reward question of novel object approach. Presenting a novel stationary plant, for example (different from the familiar leaves in the moving condition), might provide more detail on the specific foraging value of neophilic behavior. Despite these limitations, we consider the finding of cross-modal preferential approach to neutral novel stimuli (as opposed to neutral familiar stimuli) to provide an important foundation for investigations into the relationship between formative social experience and ecologically relevant traits such as neophilia in more specific contexts.

Either competitive experience and/or observation of socially dominant individuals may influence novel stimulus approach through a winner/loser effect (Frost et al., 2007). For example, blue-footed booby *Sula nebouxii* nestlings have been shown to retain early life intrabrood rank even if the subordinate partner grows to outweigh the dominant partner, and

309 behave according to their role in intrabrood hierarchy when confronted with novel dyadic
310 partners (Drummond & Osorno, 1992). In turn, barnacle goose *Branta leucopsis* goslings
311 experiencing early life success as subordinates (defined by lack of aggressive response from
312 siblings) were more likely to continue to attempt subordinate gestures in later interactions (Black
313 & Owen, 1987).

314 Arabian babblers are known to engage in object-play in the form of “tug-of-war” (Pozis-
315 Francois, Zahavi, & Zahavi, 2004), from approximately 3 weeks after fledging. Novel objects
316 may evoke a similar monopolization attempt; in agreement, Arabian babblers have been
317 characterized as inquisitive, and initiate play behaviour by examining objects encountered during
318 foraging, and choosing partners most similar in rank (Pozis-Francois et al., 2004). Social rank
319 has been found to influence roles in wrestling and chase based play, with dominant individuals
320 taking the aggressive role and dominant individuals are found to initiate play more frequently
321 (Pozis-Francois et al., 2004).

322 If novel stimuli represent risks, early, frequent approaches may signal and communicate
323 ability and contribute to (and be caused by) social prestige in babblers (Zahavi, 1995). As in the
324 winner/loser effect paradigm, this may be both cause and effect. The presence of dominant
325 individuals may inhibit the approach of subordinates (Drews, 1993; Soma & Hasegawa, 2004),
326 and dominants may signal dominance by monopolizing resources – including opportunities to
327 display quality to group members and eavesdroppers through assuming risk associated with
328 novel stimuli (Zahavi, 1995). These paradigms are not mutually exclusive. If dominant
329 individuals initiate object based play through exploration of objects, as suggested by Pozis-
330 Francois et al. (2004), novel stimuli may represent a high risk/high reward gamble.
331 Monopolization may be preferable both as a display of condition through self-exposure to risk

(Zahavi, 1995) and as an opportunity to control a potentially rewarding object or play competitively. Stöwe et al. (2006) suggested that showing off by males may be a reason for their neophilia in mixed sex exposure trials. In our study, all groups were of mixed sex. Repeated winners in resource monopolization may be established among siblings from an early age (Carlisle & Zahavi, 1986); dominants may reinforce dominance by relatively frequent and rapid approach to novel stimuli and subordinates may reinforce subordination by displaying behavioural inhibition.

Since daily weight data was not taken, the relative condition of each bird during testing was not possible to estimate. The context dependent neophilia of low-ranking or poor-condition individuals may drive lower ranking birds to risky behaviour only after a threshold of hunger has been reached. This tactic may manifest as a blackmail tactic in the Arabian babbler's close relative, the Pied Babbler (*Turdoides bicolor*) (Thompson et al., 2013): birds in that study were fed bits of mealworm *ad libitum* at the beginning of each observation session. In contrast, in our study, since only small amounts were fed initially and trials did not begin until after normal foraging behaviour had resumed, we do not consider that individuals were satiated.

Neophilic and risk seeking behaviours have been consistently linked with juvenile or adolescent individuals (Greenberg & Mettke-Hofmann, 2011). Our results show that age class was the strongest predictor of approach speed, with developmental stage negatively predicting latency. Juvenile/adolescent individuals are physically mature (or nearly so) but may be naïve relative to adults. Arabian babblers typically disperse later in life, beginning around 2 years of age (Zahavi, 1990), though one female in this study was subsequently observed to disperse at approximately one year of age. Arabian babbler young are more likely to engage in object play behaviour than adults (Pozis-Francois et al., 2004) and dominance displays become more subtle

and less aggressive in older babblers (Carlisle & Zahavi, 1986). Fledglings are more naïve relative to juveniles, and so may have experienced more noise in the environment with regard to novel vs familiar stimuli: experimentally presented novel objects may have been less attractive because many more objects in the environment are novel for younger individuals. Juveniles, with more experience and improved motor skills, may also simply be less vulnerable to the costs of risk taking, as well as being more mobile and independent of adults relative to fledglings (e.g. Ridley, 2007)

The finding that an adult babbler presence predicted more frequent approach, particularly in fledglings, allows for several non-mutually-exclusive hypotheses. It may be that risk assessment influences novel stimulus investigation, as well as observational learning. Subordinate adult Arabian babblers have been shown to act as scroungers more frequently than dominants, though they were also better innovators of novel foraging strategies (Keynan et al., 2014). Though younger birds may be more neophilic or exploratory (see below), adult interaction with a novel stimulus may have a strong influence on young. Social learning, particularly between juveniles and adults, influences foraging and feeding behaviour in a wide variety of species (Lefebvre & Bouchard, 2003) and proximity to and observation of a conspecific influences novel object approach and exploration in several social bird species (Langen, 1996; Fritz & Kotrschal, 1999; Huber, Rechberger & Taborsky, 2001, Griffin & Boyce, 2009, but see Griffin et al., 2013 on social inhibition of neophilic behaviour). The role of adult presence in facilitating approach demonstrates a decreased threshold of caution which affects frequency of and latency to approach, which may support a risk-averse hypothesis, as the young may confirm the low risk value of a novel stimulus through observation of an adult in proximity to the novel stimulus. If novelty is both risky and desirable, dominant young may be signaling

and showing off (Zahavi, 1995) by exposing themselves to unknown risk (Stöwe et al., 2006). A confound in this interpretation is that fledglings (as compared to juveniles) are nutritionally dependent on adults (Ridley, 2007) and as a consequence are rarely distant from an adult. In a free-ranging population it is unusual to observe fledglings without adult presence.

The preference for novel to familiar stimuli, particularly among juvenile birds, combined with the apparent spatial monopolization of novel stimuli by higher ranked individuals, strongly suggests that novel items are inherently attractive, supporting the risk-seeking hypothesis. The finding that adult presence lowers the threshold for approach highlights the risk-taking aspect of approaching an unknown quantity. We suggest that the frequent and relatively rapid novel object approach by dominant Arabian babblers may be a social tactic. Further research on context dependency (e.g. testing individuals in isolation) will be necessary to support this argument, but approaches to novel stimuli as potential resources or danger, may reinforce a rank, or the presence of dominant individuals may inhibit the neophilic approach behaviour of subordinate individuals in a priority of access model of hierarchy.

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