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Social conformity affects experimental measurement of boldness in male but not female monk parakeets

(*Myiopsitta monachus*)

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Abstract

The standard approach for characterizing boldness rarely considers the influence of social environment on the expression of boldness in group-living animals. We studied a wild-caught, captive population of monk parakeets (*Myiopsitta monachus*) to investigate the impact of conspecific presence on boldness — a personality trait in monk parakeets — in a controlled environment. We quantified seven boldness metrics across three types of behavioural assay: novel object, emergence, and predator exposure tests in the presence of a companion pair of flock mates. Because of the high degree of sociality in this species, we hypothesized that the presence of companion birds would facilitate the focal individuals' behavioural responses (i.e., increase the average boldness level). We found that behavioural response in a risky foraging context was inversely correlated between solitary and social condition in males, but not in females. Our results have implications for characterizing sex-specific differences of risk-taking behaviour in social animals.

Keywords

novel object test, emergence test, predation risk, latency to eat, neophobia, shyness, personality.

1. Introduction

Boldness is apparently a universal personality trait evident throughout various animal taxa (Wilson et al., 1994; Carere & Maestripieri, 2013), and is usually defined as consistent individual differences in propensity to face potential threats in the environment, such as those involved in information gathering, or access to resources (Reaney & Backwell, 2007; Dammhahn & Almeling, 2012). In this framework, animals are usually exposed to risk-related situations solitarily so that researchers can characterize individual variation by excluding extrinsic factors in the environment (Webster & Ward, 2011). However, social animals are more likely to encounter potential risks in the presence of their fellow conspecifics. For instance, sociality in birds is a prevalent phenomenon. More than eight percent of avian species are cooperative breeders (Jetz & Rubenstein, 2011), many more live in extended family groups (Brown & Brown, 1981), and at least 21 percent of all avian taxa are known to participate in mixed species flocks either seasonally or year round (Gill & Donsker, 2014; Zou et al., 2018). Thus, birds not only represent a suitable model system to examine the behavioural consequences of sociality on the bold-shy continuum, but such research is necessary to understand the ecological role of boldness expression in birds as a taxonomic group.

1.1. Varied influences of social partners in avian boldness expression

A complication in discerning this complexity is that the vast majority of boldness testing, especially in birds, occurs in experiments where subjects are tested solely in solitary conditions (Webster & Ward, 2011). However, expanding interest in how boldness interacts with decision-making in birds underscores the reality that social environment is a central factor in the expression of boldness as a risk-taking strategy (Harel et al., 2016; Hua et al., 2016; Jolles et al., 2016). Presence or actions of group members can reduce the expression of risk-taking behaviour in an individual (e.g., social inhibition; raven, *Corvus corax*, Stowe et al., 2006; zebra finch, *Taeniopygia guttata*, Mainwaring et al., 2011; Indian mynah, *Acridotheres tristis*, Griffin et al., 2013). Conversely, group members' participation may also facilitate the expression of risk-prone phenotypes (e.g., kea, *Nestor notabilis*, Huber et al., 2001; great tit, *Parus major*, van Oers et al., 2005; barnacle goose, *Branta leucopsis*, Kurvers et al., 2012). Finally, individuals' risk-taking behaviour may conform to the behaviour of others in a social setting, such

that risk-prone individuals become less so in the presence of a risk-averse individual, and vice versa (Gouldian finch, *Erythrura gouldiae*, King et al., 2015). In avian species, facilitative or inhibitory effects of sociality can be crucial for successful resolution of risky encounters such as avoiding predator encounters (Lazarus, 1979; Boland, 2003), locating and utilizing food resources (Soma & Hasegawa, 2004; Jackson et al., 2008), and exploration of novel environments (Grigor et al., 1995; Sieving et al., 2004).

Sex also plays a key role in the expression of boldness towards risky stimuli (Schuett & Dall, 2009; Schuett et al., 2010). For example, repeatability of boldness response can be dependent on the sex of the individual being tested; in some studies, male boldness was highly consistent (e.g., zebra finch, Schuett & Dall, 2009) whereas in other tests females exhibited high consistency (e.g., jungle fowl, *Gallus gallus*, Favati et al., 2015). Sexes may also diverge in relative boldness as one sex becomes bolder than the other sex (zebra finch, Mainwaring et al., 2011; wandering albatross, *Diomedea exulans*, Patrick et al., 2013). More importantly, mate choice and reproductive success can be modulated by the boldness of the opposite sex (zebra finch, Schuett et al., 2011; great tit, David et al., 2015; African penguin, *Spheniscus demersus*, Traisnel & Pichegru, 2018). In all of these cases, the social environment acts as a setting within which these sex-specific effects transpire. Although a few of these studies has touched upon the importance of sex on the expression of boldness traits across social context (Schuett & Dall, 2009), we are yet to fully understand all the variegated ways that sex can influence risk-taking behaviour in animals with rich social lives.

1.2. Study objectives

To this end, we studied the expression of boldness in a highly gregarious parrot species, the monk parakeet (*Myiopsitta monachus*), with and without conspecific presence. The social complexity of this species, like other *Psittaciformes* (Sewall, 2015; Cussen, 2016), is characterized as extreme among major vertebrate taxa and heavily influences the species' life history (Hobson et al., 2012). The monk parakeet is a medium-sized parrot species native to South America, but also living in many introduced populations across the globe (Avery et al., 2012). Living in close-knit groups year-round, it exhibits communal roosting, foraging, and nesting behaviour (Collar, 1997, Pepperberg & Shive, 2001). Communal nest sites are occupied by reproductive pairs or triads during the breeding season (Strubbe &

Matthysen, 2009), and are used for roosting outside of the breeding season (Eberhard, 1998). This facilitates the emergence of strong social bonds within groups, where individuals tend to form dominance hierarchies (Hobson et al., 2012), and help their kin in raising offspring (Homburger et al., 2008). Their social structure exhibits strong temporal stability in interaction patterns despite the fission-fusion dynamics in flocks (Hobson et al., 2014). The presence of high social cohesion and complex group dynamics make the monk parakeet an important model organism for examining the effects of social context and sex on the expression of avian personality traits. Furthermore, it broadens the number of species examined both with social and solitary personality tests, which will undoubtedly advance our understanding of how boldness is expressed in and out of groups for taxa across the continuum of social complexity.

The main goal of this study was to investigate the presence of sex-specific expression of boldness across different social situations. Given that the study species is intensely social — foraging, roosting and breeding in large flocks and likely keeping relationships with individuals over many years — we sought to evaluate whether boldness measures observed in standard solitary personality tests were consistent with results obtained in a group context. Using the same set of individual birds that were tested in a different year (reported in Kerman et al., 2016), we evaluated the effects of conspecific presence on the same standard risk-taking metrics across three behavioural assays for each sex: novel object, emergence in a new environment, and predator exposure tests. We conducted social assays of boldness where test subjects were accompanied by a pair of companions with mid-level boldness scores (with respect to the study flock), and compared boldness responses between the two social settings in this paper.

We assessed all three main types of social mechanisms: facilitation, inhibition, and conformity as well as the role of sex in boldness expression. To assess direct facilitative or inhibitory effects, we looked at the change in overall boldness levels of birds across social context (solitary vs. social). For conformity, we looked at the correlation of individual boldness scores between contexts (solitary vs. social). Presence of a negative correlation was accepted as an evidence for conformity since individuals shifted their risk-taking behaviour in response to their social setting, conforming to the boldness levels of their mid-level conspecifics (i.e., bold individuals becoming shy; shy becoming bolder). Presence of a positive correlation

between contexts was also considered an evidence for conformity only if the range of risk-taking response decreased considerably in the presence of conspecifics. If that was the case, individuals, though retaining their relative ranks, still conformed to the behavioural scores of their companion birds. Since male and female monk parakeets appear to respond similarly towards novel stimuli in a solitary condition (Kerman et al., 2016), we expected to see no sex-specific change in boldness scores in individuals retested in both solitary and social conditions.

2. Material and methods

2.1. Study population and housing

We studied a captive population of monk parakeets ($N = 41$; 21 females and 16 males) at the USDA/APHIS Wildlife Research Centre, Florida Field Station, Gainesville, FL, USA. At the time of the study, the parakeets had been in captivity for 6 years. We held them in communal cages as mixed-sex flocks with food and water, ad libitum. Since birds lived in pens of 2 to 6 individuals near all other flock members in the same facility since capture, and were transferred and mixed among communal cages intermittently over the years, we assumed the levels of familiarity among individuals were equivalent across our study population. All individuals survived the testing regime and continued to be housed at the facility after the completion of this study. Birds were not allowed to breed in captive conditions. For detailed descriptions of the methodological procedures implemented for trapping, transporting and housing birds, see Kerman et al. (2016).

2.2. Experimental design

We used a fixed order, repeated-measures design to compare the behavioural output of individuals previously tested in a solitary setting (results published in Kerman et al., 2016) in the presence of a pair of companion birds (this study). We conducted social assays opportunistically in 2014, approximately a year after solitary measures were collected in 2013. Since testing the entire flock in either social or solitary conditions takes more than 2 months, we chose this design to ensure that social and solitary tests occurred in the same seasonal (and hormonal) conditions, and to minimize the likelihood of habituation or testing fatigue. We applied three types of behavioural assays, as detailed below, that captured a total of seven boldness metrics: novel

object, emergence, and predator exposure tests (Table 1). All observations were done by KK.

2.3. Forming companion pairs

We selected eight individuals (four females, four males) to be used only as companions during the assays; these individuals were not themselves tested in the social assays. Companion birds were selected because they expressed mid-level behavioural scores in solitary tests (Kerman et al., 2016). We housed companion birds in mixed-sex dyads across four cages, and placed them in their cages two weeks prior to the beginning of behavioural assays. We maintained the same male–female companion pairs throughout the study; three of these pairs were randomly assigned to birds tested in novel object tests, while the remaining pair was used as the sole companion pair for emergence and predator exposure tests. We decided not to switch companion pairs or form new ones between our trials out of the concern that frequent disruption of companion individuals could influence the behaviour of focal birds and confound trial results. For each assay, we housed companion pairs in their own cages adjacent to the focal birds being evaluated. We assume that ‘companionship’ in our study represented relatively neutral ‘presence’ of known social partners (flock mates) because we did not observe overt agonistic or courtship behaviour between companion individuals or focal and companion birds.

2.4. Novel object test

We conducted novel object tests in three small-sized cages that were visually but not acoustically separated from one another by opaque sheets ($1.8 \times 1.2 \times 1.2$ m; Figure 1). Each cage contained two brown terra cotta plant saucers to provide food and water. We placed four large perching branches of equivalent dimensions inside the experimental cages. Each focal bird’s cage was adjacent to the cages of its assigned companion pair, enabling all three birds to maintain visual and aural but not physical contact during trials.

We started each week by transferring three randomly selected test birds to their experimental cages, where they were acclimated to the testing aviary for four days prior to testing (days 1–4). Subjects were assigned to test cages in a randomized fashion. We tested birds on day five, then placed them back to their original cages on the same day. We implemented a two-day recovery period (days 6 and 7) before the next round of trials on a new set of birds the following week.

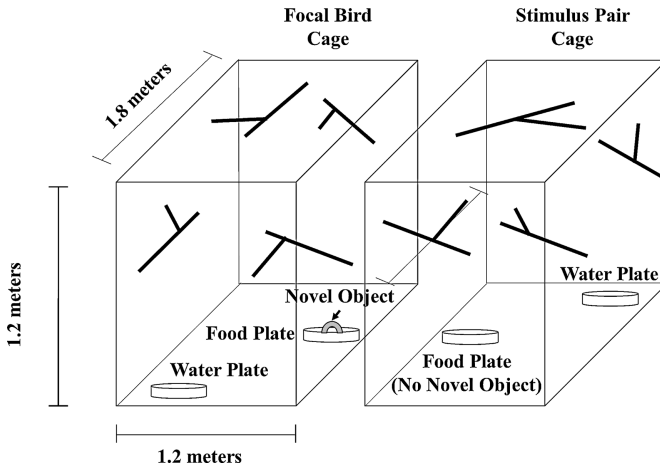


Figure 1. A diagram of the novel object arena. Thick lines represent branches and twigs inside the cage.

On days one through four of the novel object tests, we placed food saucers containing maintenance diet of seeds in the cages at 0830 h and removed them at 1630 h each day. Both focal and stimulus birds were subjected to the same protocol. On test day (day 5), we placed food plus novel objects within each food saucer, and presented them to focal birds at 0830 h. Only focal individuals received a novel object inside the food saucer; social companions had only food inside the saucer. Novel objects varied from the ones used in the solitary assays published previously (see Kerman et al., 2016). We used a combination of a plastic bag clip and a rubber ring as novel stimulus. Once the food cups were placed inside, we started videotaping the focal individuals for 90 min by using Panasonic HCV100M cameras situated in front of the test cages. No human observer was present for the remainder of the test. We quantified four behavioural metrics, as detailed in Table 1. All trials were completed by noon.

2.5. Emergence and predator exposure tests

Emergence and predator exposure tests were conducted in a medium-sized aviary ($1.2 \times 1.8 \times 2.5$ m, Figure 2). The aviary was located at a different section of the research facility than the one used in the previous study (see Kerman et al., 2016), and maintained the same dimension and design. We placed eight branches inside the aviary. One side of the aviary was

Table 1.

List of behavioural measures used, and the experimental setting within which the measures were captured (adapted from Kerman et al., 2016).

Behavioural measure	Experimental setting
Latency to enter the novel environment and perch on a branch after the opening of the release cage door. Quantified as total number of seconds.	Emergence test
Latency to consume once the food saucer, with a novel object situated in the middle of the saucer, is placed in the test cage. Quantified as total number of seconds until the bird pecks at seeds for the first time.	Novel object test
Proportion of time spent feeding during the test period. Feeding activity involved handling and consuming while in close proximity to the food saucer. Quantified as total number of seconds spent feeding, divided by the total test period in seconds.	Novel object test
Foraging rate was quantified as the total number of pecks at the food source over the time spent foraging during the trials (seconds). Individuals bobbed their heads in a distinct pattern when pecking consecutively, facilitating the quantification process.	Novel object test
Total number of feeding approaches over the entire test period. Counting of feeding approaches started when the bird made its first successful feeding approach. Each feeding approach ended when birds fled to a branch or moving approximately 30 cm away from the food saucer.	Novel object test
Total number of vocalizations while exposed to a predator during the test. Quantified number of distress calls when the predator is in the visual range.	Predator exposure test
Number of flights when exposed to a predator; quantifying each distinct flights and hops started when the bird left its perch and ended when bird landed on another perch.	Predator exposure test

Please see Kerman et al. (2016) for detailed information about the selection of behavioural assays and associated metrics.

completely covered with opaque material to hide the presence of human observers during behavioural trials. We mounted a release cage on the opaque wall with a rope attached to its door, enabling us to introduce focal birds inside the test arena at a distance. We transferred the social companions two weeks prior to the beginning of personality trials into a viewing compartment separated from the focal bird test arena by a thin mesh barrier. The viewing compartment had the same dimensions as the test arena.

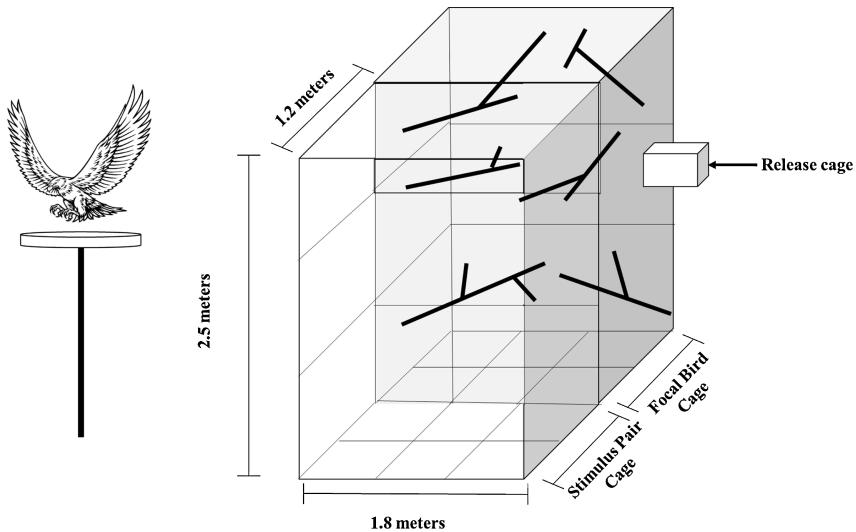


Figure 2. A diagram of the emergence and predator exposure arena. Thick lines represent branches and twigs inside the cage. The side coloured in dark grey depicts the opaque cover behind which the observer stands.

We placed a well-preserved sharp-shinned hawk (*Accipiter striatus*) specimen outside the aviary as a proxy for a real predator encounter, and hid it behind an opaque sheet until the beginning of the exposure period. Ecological information regarding avian predation activities on introduced monk parakeet populations in North America is extremely limited (Avery et al., 2012). Nevertheless, observations in their native habitats shows that some members of owl and hawk families could regularly be found occupying monk parakeet nests in South America, acting as nest predators (Martella & Bucher, 1984), and observations on invasive monk parakeet populations in North America showed that they emit alarm calls when they have detected an aerial predator (South & Pruett-Jones, 2000). Moreover, the sharp-shinned hawk is a relevant avian predator model as they are year-round residents in the native habitats of monk parakeets in South America, and they have overlapping distribution with introduced populations of monk parakeets in Florida (where our study birds were captured) except the summer months (White et al., 2018).

Tests began by placing a focal bird inside the release cage. We implemented a five min acclimatization period so that subjects were calm enough before the beginning of the trial. As soon as the cage door was open, we

measured the latency of focal birds to enter the novel environment as the sole metric for the emergence test. Once focal birds entered the test arena, we waited for 20 min to allow focal birds to habituate to their surroundings. All individuals initiated preening well before the habituation period ended, which was considered a relaxed behaviour (Blumstein, 2003). At the end of the habituation period, we exposed the predator model by pulling a cord attached to the sheet in front of the predator model. We quantified the following behavioural output in the first minute that the predator was exposed: number of distress calls and number of flight attempts after exposed to predator models (Table 1). Distress calls were determined using the previous information published on monk parakeet vocalization (Martella & Bucher, 1990). At the end of each trial, we replaced the sheet, hiding the predator model from view. All birds reacted immediately when the predator behind the plastic cover was exposed by emitting distress calls and initiating short bursts of flight. They resumed normal behaviour when the cover was replaced at the end of the observation period. Similar to novel object tests, we filmed behavioural responses through cameras stationed behind a small opening in the opaque barrier. Behavioural trials continued from 0830 h to 1130 h, enabling us to test 2–3 birds a day over 11 days.

2.6. Statistical analysis

We used R packages “multigroup” for principal component analysis, “stats” for correlation analysis, and “ggplot2” for graphical output (R Team, 2002; Wickham et al., 2013; Eslami et al., 2015).

2.6.1. Identifying behavioural axes

We relied on principal component analysis (PCA) to assess how multiple, commonly used risk-taking measures from different assays were related to one another. This approach has previously been used effectively to characterize personality variation in monk parakeet in social isolation (see Kerman et al., 2016). We implemented a multi-groups principal components analysis (mgPCA; Thorpe, 1988), a statistically more robust version of standard PCA where behavioural observations obtained from both solitary (which were published in Kerman et al., 2016) and social trials could be pooled and analysed together. Multi-groups PCA generates variance-covariance matrices by centring data within each treatment (solitary and social) while retaining individual identities (corresponding to the same individuals; Krzanowski, 1979;

Abdi et al., 2013; Huang et al., 2016). Using mgPCA, we could obtain component axes comprised of combined data from both contexts (in order to identify distinct latent behavioural traits) and, in turn, we could then parse the data into subsets according to the treatment group to conduct inferential analysis. In order to satisfy the assumptions of normality for PCA, we applied a log-normal transformation of latency and rate measures (Girard et al., 2004; Krause & Naguib, 2011), square-root transformation of count measures (Moretz et al., 2007), and arcsine square-root transformation of proportional measures (David et al., 2011); normality was confirmed with normal probability plots. Principal components (PCs) with Eigenvalues < 1.0 were excluded from further interpretation (Kaiser, 1960). In assessing the relative importance of component loadings on each PC, we used a cut-off value of ≥ 0.4 (Stevens, 1992; van den Brink et al., 2012).

According to our analysis, only PC1 and PC2 (i.e., boldness during foraging and predator encounter, respectively) retained comparable loading values across solitary and social conditions (i.e., behavioural measures that had high loading values were similar across contexts), thus representing distinct latent behavioural traits (Table 2). Therefore, we focused our inferential analyses on those two components.

2.6.2. *Evaluating social facilitation and inhibition*

We looked at whether the presence of companion birds increased (i.e., facilitated) or decreased (i.e., inhibited) the overall expression of risk-taking behaviour by comparing boldness scores obtained in social isolation to scores obtained in conspecific presence (for all individuals, then for each sex separately). Since component scores were calculated through linear combinations of centred behavioural measures, any analysis of variance could fail to detect the overall direction of change in risk taking behaviour. We therefore used Wilcoxon signed-rank test — a non-parametric test suitable for repeated measurement on the same set of individuals — on each metric that had loadings equal or larger than 0.4 in the components. Finally, we adjusted the significance level using the Bonferroni correction ($\alpha = 0.003$) to avoid the inflation of Type-I error.

2.6.3. *Evaluating social conformity*

We looked at whether bold individuals became shy, and vice versa when behavioural assays were implemented with companion birds. We obtained component scores for PC1 and PC2, and compared each component's scores

between solitary and social conditions using Spearman's rank-order correlation to detect rank changes (Wilson & Godin, 2010; Gyuris et al., 2012). We ran repeated correlation analyses by first pooling individuals from both sexes, and then with each sex separately.

3. Results

In all of our behavioural assays (novel object, emergence and predator exposure tests), monk parakeets responded to risky stimuli within the observation period (Table 2). In the social treatment, sexes did not differ significantly from one another in any of our seven metrics used in the behavioural assays (see Appendix).

3.1. Social facilitation/inhibition

Considering the hypotheses that the presence of companions would either facilitate or inhibit boldness behaviour, we did not find a unidirectional change associated with social environment in any of the behavioural measures loaded on PC1 and PC2 (Table 3).

3.2. Conditional change in boldness

Considering the hypothesis that individuals should react conditionally to conspecifics' boldness phenotype (i.e., conformity), we did not observe a significant correlation in boldness scores across social context for either behavioural dimension when both sexes were pooled: boldness in a foraging context (i.e., PC1) and boldness in a predation context (i.e., PC2, Table 4). Males, but not females, showed an inverse correlation between social and solitary treatments for boldness response captured in a risky foraging test ($R_S = -0.67$; $p = 0.02$; Figure 3), but neither sex showed significant correlation in the predation test (Table 4).

4. Discussion

4.1. Males but not females exhibited social conformity

We found that male monk parakeets that are risk-averse in a foraging context adopted a more risk prone phenotype when conspecifics were nearby, and vice versa. Thus, males appear to conform to social partners in their presence. Females, on the other hand, failed to exhibit a similar type of conformity in their boldness response. Interestingly, this effect is despite the fact

Table 2. Summary statistics of seven behavioural metrics used in solitary and social treatments (mean ± SD), and component loadings from the group-level principal component analysis (mgPCA) of the solitary and social groups, with Varimax rotation.

Behavioural measure	Mean ± SD		PCA (Solitary)			PCA (Social)			
	Solitary context	Social context	PC1	PC2	PC3	PC1	PC2	PC3	PC4
Latency to enter the novel environment	866.7 ± 1216.3	373.8 ± 635.4	0.03	0.17	-0.57	-0.05	0.01	0.03	0.86
Latency to consume food when novel object is present	738.8 ± 1403.1	825.8 ± 1536.9	-0.60	0.03	-0.04	-0.55	0.05	0.34	0.14
Proportion of time spent feeding	0.1 ± 0.2	0.1 ± 0.04	0.01	-0.11	-0.74	-0.05	0.02	-0.88	0.03
Pecking frequency when novel object is present	0.5 ± 0.3	0.5 ± 0.3	0.54	0.07	0.45	0.63	0.04	-0.24	0.08
Total number of feeding approaches	5.9 ± 5.5	7.5 ± 6.7	0.53	-0.01	-0.14	0.40	-0.08	-0.34	0.41
Total number of vocalizations when exposed to a predator	7.4 ± 7.1	9.9 ± 17.3	0.05	0.68	0.05	0.11	0.75	-0.08	-0.23
Total number of flights when exposed to a predator	4.4 ± 4.1	3.5 ± 3.1	-0.01	0.67	-0.09	-0.11	0.69	0.08	0.18
Eigenvalues			1.84	1.68	1.17	1.9	1.28	1.2	1.12
Percentages of variance explained			27.1%	24.7%	17.2%	28.1%	18.8%	17.7%	16.5%

Eigenvalues and percentages of variance explained by each principal component (PC) is presented at the bottom of the table. Variable loadings that are ≥0.4 are indicated in italics.

Table 3. Wilcoxon signed-rank test of the effect of companions on five behavioural metrics loaded on PC1 and PC2.

Behavioural measure	Principal component	All individuals		Male		Female	
		V	p	V	p	V	p
Latency to consume food when novel object is present	PC1	243	0.50	35	0.75	100	0.59
Pecking frequency when novel object is present	PC1	350	0.21	51	0.35	139	0.41
Total number of feeding approaches	PC1	267	0.15	32	0.65	117.5	0.16
Total number of vocalizations when exposed to a predator	PC2	171	0.67	44	0.10	33	0.04
Total number of flights when exposed to a predator	PC2	200	0.23	30	0.79	78.5	0.20

Tests were conducted on pooled data as well as for each sex separately. The *V*-statistic represents the total sum of all positive ranks in the dataset. Bonferroni corrected alpha level is set to 0.003.

Table 4.

Spearman rank-order correlation analysis on PC1 and PC2 scores for all individuals, as well as for each sex.

	PC1		PC2	
	R_S	P	R_S	P
All individuals	−0.12	0.49	−0.10	0.65
Males	−0.67	0.02	−0.01	0.99
Females	0.19	0.42	−0.14	0.55

that males and females exhibited similar levels of response when exposed to a novel object in the context of a foraging task.

Conformity reflects individual preferences that are modified after the interaction with a group member, even if the adopted behaviour is the less-preferred one (Galef & Whiskin, 2008). Initially described in humans and non-human primates (Cialdini & Goldstein, 2004; Whiten et al., 2005; Dindo et al., 2009; van de Waal et al., 2013), conditional change in behaviour in response to the actions of conspecific individuals has been documented in other vertebrate groups such as rodents (Galef & Whiskin, 2008; Jolles et al., 2011), birds (Aplin et al., 2015; King et al., 2015), and fish (Day et al., 2001; Webster & Laland, 2012). One of the demonstrated selective advantages of conforming to group behaviour is acquiring behavioural norms that

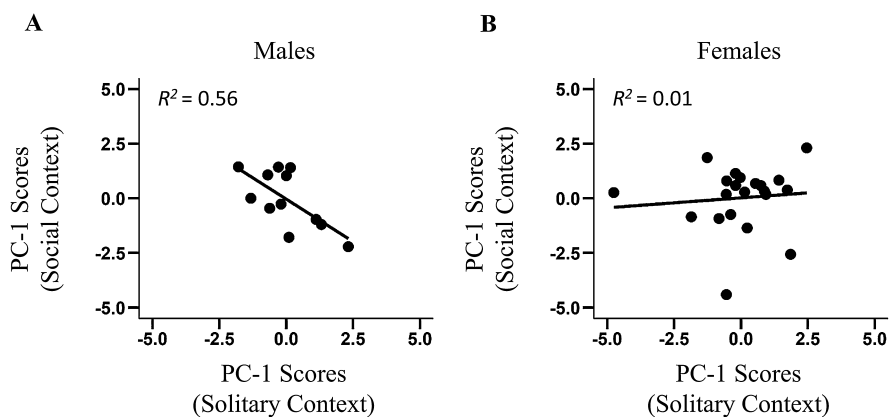


Figure 3. The linear relationship of PC1 scores between solitary and social contexts in (A) males and (B) females. The regression lines and the amount of variation explained by each regression model are presented in the figures.

help them utilize local food resources, which newly immigrated individuals rely on after their dispersal into a new social group (Vale et al., 2017). For species that show sex-specific natal dispersal patterns, we would expect individuals of the emigrating sex to have a higher tendency towards conformity in response to risk-related events, so that they can better adapt to their novel environment and maximize their fitness through observation of the local preferences in their new social groups (van de Waal et al., 2013). For example, naïve male vervet monkeys (*Chlorocebus pygerythrus*) that immigrated to a novel troop quickly adopt the alternative food option that are preferred by existing group members (van de Waal et al., 2013), while females — which is the philopatric sex — do not exhibit this similar behavioural response as they do not change groups and act instead as the main hub of social attention and directed social learning due to their long experience in the environment (van de Waal et al., 2010; Renevey et al., 2013). It is an interesting possibility that a similar selection mechanism could be involved in the male-biased conformity in monk parakeets.

Monk parakeets are known to exhibit philopatry as they tend to use the same communal nest site over multiple years (Collar, 1997, Pepperberg & Shive, 2001). They disperse from their natal site only relatively short distances (Martin & Bucher, 1993; Bucher & Aramburú, 2014), though their dispersal range is larger in non-native habitats potentially due to human-assisted introduction events (da Silva et al., 2010; Edelaar et al., 2015). Unfortunately, since monk parakeets do not show marked sexual dimorphism, there is no information from these studies about sex-specific patterns in dispersal events. While female-biased dispersal is considered the norm in birds, male biased dispersal does occur (Clarke et al., 1997) and has been confirmed in Psittaciformes (Caparroz et al., 2009). We therefore propose male-biased dispersal in monk parakeets should be considered in a future study.

4.2. Potential confounding factors

While we are quite confident in the validity of our findings, documentation of animal behavioural syndromes is complex and very popular now. In order that we may provide insights that can strengthen future study designs, we undertake a careful examination of our procedures. One potential factor that could influence the observed boldness response in this study is the size of the social unit used during assays. How individuals respond to risky conditions in different group sizes depends on the taxonomic and ecological context within which the behaviour arises. In fish, for example, larger

groups of guppies (*Poecilia reticulata*) tended to exhibit greater conformity in entering a novel environment and foraging on a novel food item (Day et al., 2001). In contrast, smaller groups of perch (*Perca fluviatilis*) were more likely to conform to the overall risk-taking behaviour in emergence and predator exposure tests (Hellström et al., 2011). Also in birds, Kurvers et al. (2011) found that boldness affected decision making in barnacle geese when tests were conducted in pairs but not in larger groups. Although some evidence suggests that multiple monk parakeet pairs readily join others to form larger groups during food acquisition (e.g., fission-fusion dynamics, Hobson et al., 2014), our social setting (3 birds) characterizes a typical monk parakeet social sub-unit. Therefore, while we stress that the numerical definition of ‘social condition’ for any species in a study like ours should be made with care, we have no reason to believe that our social group construct was inadequate to detect the influence of social context on personality variation.

The role of a physical barrier between companion and focal bird cages, where some species were tested adjacent to a stimulus bird cage (e.g., great tit, van Oers et al., 2005), while others tested within a social group (e.g., Gouldian finch, King et al., 2015) should be fully investigated for an accurate representation of boldness in a given species (Kerman et al., 2018, in press). For example, housing in the same compartment can trigger agonistic interactions at the food cup, where dominant individuals displace subordinate birds, ultimately confounding their boldness response. In some cases, dominance rank successfully predicts the positioning on a bold-shy continuum in a foraging task (Dingemanse & de Goede, 2004; Dahlbom et al., 2011; David et al., 2011), which gives the researchers enough confidence to discard it as a confounding effect. However, this association between boldness and dominance status is not universally true (Fox et al., 2009; Kurvers et al., 2009), and we did not know in advance if dominance in monk parakeets is related to their boldness scores or sex-specific responses during risky foraging. Under this uncertainty, testing focal birds in a separate compartment from companion pairs was the most rational approach, as even a partial cage division introduced recently can significantly reduce aggression and hierarchy-related anxiety in captive animals (Tallent et al., 2018). Further, monk parakeets housed in different cages lived in visual and aural contact with all other population members (small cages grouped together within a protected open-air aviary); thus individuals were already accustomed to this

sort of physical arrangement. We therefore think that the effect of dominance related aggression is likely to be extremely limited or absent in our study.

Finally, we would like to consider two potential non-random influences on our ability to detect a true treatment response: (1) carryover effects (influences of solitary test protocols on the follow-up social test responses); and (2) chronic impacts of an extended period in captive conditions. A year-long interval occurred between solitary and social assays. On the one hand, this long period likely eliminated carryover effects of the solitary trials into the social trials. However, this lengthy period could increase the potential for systemic shifts in extrinsic and intrinsic factors (e.g., stress, illness, environmental or caging changes; van Horik et al., 2017) affecting individual responses flock-wide. Through memory and experiences accumulated during long-term captivity consistent divergent alterations in behavioural response of individuals or sexes could have occurred (LaDage et al., 2009; Dingemanse et al., 2012). But while we acknowledge these possibilities as serious considerations in future research designs, especially in newly formed captive flocks, we do not think they were important in our study. The environment of our birds had been very stable over their 6 years of captivity prior to the solitary measures. The birds' daily and weekly maintenance regimen continued under the exact same animal care protocol across the entire time-period encompassing the solitary and social tests, with no systematic alterations in caging, feeding or health care. We still worried about other lesser unknown effects (e.g., undetected predator threats, unmeasured climatic shifts, etc.), and considered using a stronger design (involving splitting the flock in two halves with social and solitary treatment applied to each half in different orders) to control for unknown temporal shifts. But we also had constraints on space and cage availability in undisturbed areas of the site, and a critical requirement for seasonal consistency (see Methods) such that the latter design could not have been implemented without introducing other, more serious, complications. All in all, we are confident that we chose the strongest and least biased design for our study, given local constraints; that major unknown biases were adequately controlled by the strict flock management regimen. We provide these comments to encourage attention to achieving the strongest designs when testing behavioural outputs in higher vertebrates in general, and carefully considering both hierarchical formation and size of social groups in further tests of sex influences on risk-taking behaviour in this and other vertebrates.

5. Conclusion

The nature of social effects on personality expression are complex and therefore is not simple to characterize. Even though animals exhibit variation in personality, individual behavioural patterns are mediated by a variety of social interactions in group-living organisms (Farine et al., 2015; Vander Wal et al., 2015). Thus, ignoring sociality in quantifying individuals' risk-taking behaviours might inaccurately reflect the ecological and evolutionary implications of boldness in natural populations (Webster & Ward, 2011). Here, we provide support for the importance of sociality in the investigation of animal personality traits and its relation to sex-specific foraging behaviour in groups (Toscano et al., 2016). Our study contributes to the small body of literature that documents the role of social context on personality traits and that either sex might be more responsive to social cues in a risk-taking context than the other. Our use of parallel social and solitary testing contexts is applicable in most taxa and across the spectrum of different personality axes (boldness, activity, aggression, etc.) and may help in achieving a general framework of social context effects on personality expression.

Many parrot species, including the monk parakeet, are either intruded upon by development in their native ranges or released into novel environments through human intervention (Russello, 2008; Strubbe & Matthysen, 2009; Peck et al., 2014; Lopes et al., 2017). In such species, coping with novel challenges such as food-finding, which is often dependent on more extreme risk taking behaviours (Martin & Fitzgerald, 2005; Short & Petren, 2008; Lapiedra et al., 2017), can be strongly tied to personality expression in a social unit (Aplin et al., 2014). Therefore, across applied or theoretical undertakings where behavioural typing may be a useful tool, tests in a social group may be better suited, and should certainly be included, in evaluating personality trait influences on population parameters of social species (Evans et al., 2010; Mainwaring et al., 2011).

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Appendix

Table A1.

Sex differences in behavioural metrics captured in the social treatment.

Behavioural measures	<i>W</i>	<i>p</i>
Latency to enter the novel environment	477	0.72
Latency to consume food when novel object is present	454.5	0.51
Proportion of time spent feeding	607.5	0.17
Pecking frequency when novel object is present	576	0.34
Total number of feeding approaches	472	0.67
Total number of vocalizations when exposed to a predator	526	0.77
Total number of flights when exposed to a predator	446.5	0.44

Wilcoxon signed-rank test of the effect of sex on the behavioural metrics measured during assays conducted in the presence of conspecifics. Bonferroni corrected significance level is set to 0.01.