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Functional traits including interspecific sociality affect mobbing behaviour in a bird community of southern China

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Abstract

Mobbing is a prevalent anti-predatory behaviour in birds where prey actively engage in harassing predators. Functional traits have been shown to affect prey species' tendency to engage in mobbing, but empirical studies have largely neglected to assess the influence of some other potentially important functional traits, such as intraspecific and interspecific sociality, on mobbing or measured different aspects of the behaviour. In this study, we performed playback experiments that elicited mobbing responses from a forest bird community in southern China, to investigate the influence of body mass, foraging strata, as well as intra- and interspecific sociality, on the prevalence of mobbing, as well as the intensity of aggression and vocalness. We found that species with small body masses engaged in more frequent and intense mobbing behaviours. Notably, interspecific sociality was negatively associated with birds' mobbing prevalence and tended to be negatively associated with vocalness.

Keywords

functional traits, interspecific sociality, mobbing intensity, mobbing prevalence.

1. Introduction

Mobbing is an anti-predatory behaviour in which prey surround the predator or intruder and produce conspicuous behaviours, such as producing stereotyped movements and alarm calls (Curio, 1978; Flasskamp, 1994; Dutour et al., 2017a). Mobbing is costly as it consumes time and energy, and individuals involved in mobbing may be attacked by the mobbed predator or an additional one (Dugatkin & Godin, 1992; Krams et al., 2007). There are several benefits, however, that can potentially offset these costs, including forcing predators to 'move on', silencing offspring, teaching offspring through cultural transmission, and recruiting conspecific and/or heterospecific individuals to dilute the risk (Carlson & Griesser, 2021). Overall, the behavioural decision to engage in mobbing involves a complex balance between taking risks and enhancing fitness (FitzGibbon, 1994; Berzins et al., 2010), which are in turn affected by a suite of external and intrinsic factors (Jiang et al., 2020; Bai et al., 2021).

In prey species of birds, functional traits affect the cost-benefit balance of mobbing, especially those traits that are relevant to the species' vulnerability to predation risk (Radloff & Toit, 2004; Dutour et al., 2017b; Jones & Sieving, 2019). These include body size of prey, a primary determinant of the type of predator a given species is vulnerable to (de Lima et al., 2018; Schalk & Cove, 2018), as well as the foraging strata at which a given species typically forages, which dictates its spatial overlap with predators and competitors (Hua et al., 2016; Cunha et al., 2017a). Given the importance and diversity of functional traits, it is crucial to expand analyses of mobbing to include a broader range of relevant traits.

Intraspecific and interspecific sociality are two other traits that are highly relevant to species' vulnerability to predation risk (Potvin et al., 2018; Zhou et al., 2021). Interspecific sociality (i.e., the species' tendency to flock with heterospecifics, notably in the form of mixed-species flocking) is widely considered an adaptive behavioural strategy to reduce predation risk (Goodale et al., 2017; Zou et al., 2018), as it reduces the energy individuals must expend in vigilance, often through shared responses to alarm calls, and increases foraging rates (Sridhar et al., 2009). Given that species that participate in mixed-species flocks are already in a defensive grouping, their mobbing activity might be decreased. In contrast, intraspecific sociality (i.e., the species' tendency to flock with conspecifics) may also increase the necessity of providing predation-risk-related information to mates, offspring, or other

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related individuals that are important for fitness (Griesser & Ekman, 2005; Goodale et al., 2010). For instance, Cunha et al. (2017b) found that species that live in stable groups or flocks were more likely to mob than solitaryily living species in bird communities of semideciduous forests and savannah patches in Brazil. Yet apart from this example, empirical studies have largely neglected assessing the effect of sociality on mobbing behaviours. Therefore, it is necessary to investigate mobbing in multiple species that have different social systems (Carlson & Griesser, 2021).

The relevance of species' functional traits to mobbing has mostly been studied on the tendency to mob (Hua et al., 2016; Jones & Sieving, 2019), but not on other aspects such as the aggressiveness or vocalness of the mobbing individuals. Aggressiveness implies a willingness to impose stress on the predator, while vocalness represents an inclination to inform other prey (Strnad et al., 2012), although it could also put pressure on the predator by irritating it, or by secondarily recruiting more individuals to mob. Although both types of intense behaviours can occur during a single mobbing bout and serve the same goals (such as to 'move on' the predator), they need not go hand-in-hand (i.e., it is possible to have strong vocalness coupled with low aggressiveness, and vice versa). It might be expected that some passive species benefit from aggressive or vocal species, to reduce the probability of being noticed or attacked while ensuring low predation risk themselves (Contreras & Sieving, 2011; Randler & Vollmer, 2013).

In this study, we examined how the functional traits of body mass, foraging strata and sociality affect prey mobbing behaviour in a diverse subtropical forest in southern China. We elicited avian mobbing by simulating the presence of a small-bodied understory predator with playback and an accompanying physical model, and quantified birds' mobbing behaviours using three complementary indices, including mobbing prevalence, aggressiveness and vocalness. We expected that species with a high degree of intraspecific sociality and small body size would exhibit high mobbing prevalence, intensity of aggressiveness and vocalness, because such species are more vulnerable to small predators and gain from informing their kin about predators. In contrast, we predicted that species with a high degree of interspecific sociality and a tendency to forage in the canopy would exhibit a low mobbing prevalence, and a low intensity of aggressiveness and vocal willingness, because species living in the canopy have advantages in obtaining predator information and those that regularly join mixed-species flocks are more protected from predators.

2. Material and methods

2.1. Study area, transect selection and bird surveys

We conducted playback experiments on six transects in the Nonggang National Nature Reserve (NNNR), Guangxi Zhuang Autonomous Region, near the Chinese–Vietnamese border (22°47′N, 106°95′E). NNNR is on the edge of the tropics and the vegetation type of the area is categorized as tropical monsoon rainforest (Wang et al., 2014). We selected six one-kilometer stretches of unpaved roads as transects, with the transects being at least 500 m apart (Figure 1). Transects were visited from January to July 2017, in November 2017 and in February 2018. These visits included both the breeding season (April to August) and the non-breeding season (September to March). During each month, we visited each transect, once in the morning, and once in the afternoon. We collected data on species abundance by detecting visually or aurally all individuals within 50 m of the transect as we walked it to the end, and then conducted playback experiments (64 of 170) were analyzed in a previous study on the effect of seasonality on mob-



Figure 1. The study area and transects. Inset on the top right shows the location of the research site in China's Guangxi Zhuang Autonomous Region, near the border with Vietnam. The main map shows the location of the survey transects, with base map extracted from Google Earth (image taken on July 24th 2021), and showing the numerous karst escarpments in the area.

bing (Jiang et al., 2020); here we focus on comparing species, considering all of the experiments together.

2.2. Playback protocol and scoring of recordings

To simulate the presence of a vocal predator, we prepared two collared owlet (Glaucidium brodiei) models (made by Styrofoam but covered in painted chicken feathers) and five playback tapes of its calls. Collared owlet is a small predator (around 50 g), which can be highly dangerous for birds and often makes calls during the daytime in the study area. Mobbing has been shown to be highly influenced by predator size (Templeton et al., 2005); however, we did not consider other owl or owlet species of the region because they are relatively rare and their main diets are not birds. Playback tapes of the owl calls were based on high-quality recordings from five individuals, downloaded from the website Xeno-Canto (https://www.xeno-canto. org). Each tape lasted five mins and consisted of five one-min segments, with each segment consisting of 30 s of vocalization and 30 s of silence. Both models and playback tapes were randomly assigned to the playback trials, and the amplitude of playbacks was standardized to approx. 90 dB at 1 m for the loudest part of the exemplar, which we found similar to the amplitude of owlets in the forest, judging by ear from approx. 50 m away.

We selected playback sites based on the absence of birds and distance from previous trials. For each visit to each transect, we selected the first playback site where we did not observe any birds within 30 m, so that responding species would not be affected by the species already present. We selected the next site to be 250 m from the first site, adjusting it by moving it forward if there were birds around. After the playback site was settled, we mounted the owlet model on a 3 m-tall pole, placed the pole near a tree to support the pole, and attached the speaker (model WA-35, JTS Professional) to the pole below the model. To better estimate the distance between the owlet model and mobbers in an upcoming experiment, we selected and measured four reference trees in four ordinal directions, 30 m away from the pole with a range finder. Two observers kept 10 m away from the owlet model. We audio-recorded 30 s before the experiment, and then throughout the experiment, and for 60 s following it, with a Marantz PMD 671 digital recorder and a Sennheiser ME62 omnidirectional microphone. When playback started, the primary observer (DJ) observed the surroundings and took notes on species identity, abundance, distance and behaviour while a second observer assisted the observation by reporting what he/she had seen while making the audio recording. For each responding individual that approached the model within 30 m and displayed conspicuous mobbing behaviours (such as swooping, searching, switching of perches, or perching near the model), we recorded the minimum distance to the owl model, and whether or not the bird made a mobbing call. We defined mobbing calls as vocalization types that birds consistently made after exposure to the predator model in multiple trials (Goodale & Kotagama, 2005). Individuals were not considered to be mobbing if they just showed up within 30 m but did not display any antipredation behaviour — such birds tended to move away quickly after they approached.

After the field observations, we listened to the recordings and inspected spectrograms of them using the sound analysis software Raven (version 1.3, Cornell Laboratory of Ornithology), with a Hamm Window and FFT of 512. We then extracted another variable from the recordings: the duration of an individual's mobbing call, defined as the time between its first and last recorded mobbing vocalization.

We must acknowledge that our experiments were not blinded — blinding would be very difficult to accomplish in a playback experiment in which the observer is also noting the vocal response of animals. However, this analysis is an extension Jiang et al. (2020) in which the goal was to describe the mobbing response of bird species under different levels of threats. In this fieldwork, we gathered multiple data at once, with the goal of describing the behaviour of each responding individual, leaving specific hypothesis testing for later. Indeed, at the time of the fieldwork we had not categorized the species as to their traits, so we believe this analysis is unlikely to be affected by conscious or subconscious biases.

2.3. Describing mobbing behaviour

To summarize mobbing aggressiveness and vocalness across all playback trials for each species, we first defined different categories of aggressiveness and vocalness for each responding individual in each trial, based on observations and audio recordings. We defined aggressiveness into two categories: high intensity, if a mobbing individual approached within 5 m of the owl model, or approached within 5–15 m, but also displayed long-lasting and rapid antipredation behaviours (\geq 30 s in duration), such as searching and perch-switching; and low intensity, if an individual approached within 15–30 m of the owl model and displayed long-lasting mobbing behaviour,

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or approached within 5–15 m but performed only short-lasting behaviours (Gu et al., 2017; Zhou et al., 2021). We similarly categorized vocalness as strong, if a mobbing individual produced mobbing calls with more than three isolated notes; or weak, if a mobbing individual produced a few fragmented mobbing calls. Each species was rated as highly aggressive or strongly vocal for a trial if any individual engaged in such behaviour. We then summarized the number of trials in which the species displayed high versus low intensity, or strong versus weak vocalness. Mobbing prevalence was simply the number of trials in which a species mobbed, either with high or low intensity.

2.4. Functional traits

We focused on four functional traits. Two traits were related to body size and foraging ecology: (1) body mass (in grams, de Lima et al., 2018) and (2) foraging strata, grouped into two categories: canopy and understory (Hua et al., 2016). We compiled data on these two traits from published sources (Jiang, 2007; Wilman et al., 2014) and our earlier field data from the study region. The other two traits were related to sociality, including (3) intraspecific sociality, measured as the proportion of individuals observed in pairs or mono-species flocks among all those detected during our transect surveys, and (4) interspecific sociality, measured as the proportion of individuals observed in mixed-species flocks during transect surveys (Martínez et al., 2016). We initially considered including the functional traits of diet type and foraging technique in our analyses (Jones & Sieving, 2019), but finally excluded them because they displayed collinearity with the above traits.

2.5. Statistical analyses

We constructed phylogenetically-controlled models using the 'MCMCglmm' package (version 2.33 Hadfield, 2010) in the R statistical software environment (version 4.0.2 R Core Team, 2017), which constructs generalized linear mixed models using Markov chain Monte Carlo techniques. To prepare this analysis, we followed Liang et al. (2018) to download 9000 trees for the 40 species included in our study from http://birdtree.org and extract the maximum clade credibility tree in BEAST (version 1.8.2) using its 'TreeAnnotator' tool. We modeled mobbing prevalence using a Poisson distribution with the four functional traits and the species' natural abundance (i.e., the total number of individuals of each species that we encountered in the transect surveys) as explanatory variables. Models for mobbing aggressiveness

and vocalness followed a similar structure, although they did not include species' natural abundance, and they additionally included mobbing prevalence as an offset variable. Phylogenetic relatedness was included as the random variable for all three models. To avoid spurious conclusions from rare species, we focused on species that were either encountered in more than 5% of total transect visits or mobbed during more than 2.5% of the total playback trials.

Prior to model runs, we checked correlations between predictive variables to avoid multicollinearity, and selected variables only if they had VIF values of ≤ 2 , using the 'vif' function in the 'car' package (Fox et al., 2007). For all models, we specified an uninformative prior by setting nu = 0.002 and v = 1 for both fixed and random effects. The number of MCMC iterations, burn-in period and thinning interval were set as 330 000, 30 000 and 300, respectively. After running the global models, we simplified them manually by eliminating predictive variables with p > 0.10.

3. Results

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We conducted 83 transect visits across nine months and encountered 82 species and 2732 individuals. These included 41 species (including the collared owlet itself) encountered in $\geq 5\%$ of visits. We simultaneously conducted a total of 170 playback trials, of which we analyzed data from 160 trials, as they elicited at least one species to mob. In total, 44 species and 1402 individuals responded to the owlet playback and model presentation; 16 species mobbed in $\geq 5\%$ of all trials, involving 1223 individuals (Table 1). Following our data inclusion criteria above, pertaining to the minimum number of transect encounters or mobbing responses, we included 40 species — after excluding the collared owlet — in subsequent analyses (Table A1 in the Appendix that can be accessed at 10.6084/m9.figshare.22725863).

We found that body mass had a significantly negative influence on all three types of mobbing behaviours (Figure 2A), with smaller species more likely to exhibit high mobbing prevalence ($\beta = -0.05, 95\%$ CI = [-0.09, -0.02], p < 0.001), high aggressiveness ($\beta = -0.06, 95\%$ CI = [-0.10, -0.02], p < 0.001), and strong vocalness ($\beta = -0.08, 95\%$ CI = [-0.14, -0.02], p < 0.001). Notably, we also found that interspecific sociality had a significantly negative influence on mobbing prevalence ($\beta = -2.41, 95\%$ CI = [-4.47, -0.22], p = 0.03); Figure 2B) and a marginally significant

Species	Times detected	Times mobbed	Body mass (g)	Vertical strata	Intraspecific sociality	Interspecific sociality
Forktailed sunbird (Aethopyga christinae)	94	43	6.3	High	0.30	0.05
David's fulvetta (Alcippe davidi)	90	150	13.8	Low	0.92	0.67
Pin-striped tit-babbler (Macronous gularis)	87	153	11.2	Low	0.95	0.43
Black naped monarch (Hypothymis azurea)	54	44	12.2	Low	0.52	0.22
White-bellied yuhina (Erpornis zantholeuca)	53	50	9.7	High	0.90	0.61
Yellow-bellied warbler (Abroscopus superciliaris)	48	50	6.5	High	0.78	0.33
Olive-backed sunbird (Nectarinia jugularis)	29	6	6.3	High	0.73	0.18
Rufous-capped babbler (Stachyris ruficeps)	20	76	8.4	Low	0.83	0.65
Hainan blue flycatcher (Cyornis hainanus)	19	35	13.9	Low	0.36	0.21
Black-creasted bulbul (Pycnonotus melanicterus)	18	22	63.9	High	0.67	0.00
Streak-breasted scimitar babbler (Pomatorhinus ruficollis)	16	48	25.7	Low	0.72	0.42
Red-whiskered bulbul (Pycnonotus jocosus)	15	50	29.2	High	0.92	0.02
Limestone warbler (Phylloscopus ricketti)	15	51	7.1	High	0.74	0.49
Sultan tit (Melanochlora sultanea)	12	14	34.5	High	0.68	0.36
Puff-throated bulbul (Alophoixus pallidus)	12	73	48.1	Median	0.95	0.10
Common tailorbird (Orthotomus sutorius)	12	50	8.4	Low	0.69	0.20

Functional traits, mobbing frequency and abundance of 16 bird species that mobbed in $\ge 5\%$ of all trials.

Table 1.

two individuals. Interspecific sociality is the percentage of individuals that were seen in mixed-species flocks. A full list of species that were found on more than 2.5% of transects, and also included in the analysis, is included in Table A1 in the Appendix that can be accessed at 10. 6084/m9.figshare.22725863.

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Figure 2. The effect of body mass (A) and interspecific sociality (B) on mobbing behaviours. We included significant and marginally significant variables (p < 0.10) only. Dots represent the mean effect size, while whiskers represent the 95% confidence interval.

negative effect on vocalness ($\beta = -2.96$, 95% CI = [-6.26, 0.96], p = 0.092; Figure 2B), indicating that species regularly participating in mixedspecies flocks were less likely to respond to mobbing or exhibit intense vocal behaviours. Additionally, we found a significant positive effect of species abundance on mobbing prevalence ($\beta = 0.01$, CI = [0.006, 0.20], p = 0.002). The rest of the variables, which included foraging strata and intraspecific sociality, were not significant for any of the three aspects of mobbing studied (all p > 0.15).

4. Discussion

We found that different aspects of mobbing in a forest of southern China were affected by functional traits, including some traits often considered in mobbing studies, such as body size, and others less studied, such as interspecific sociality. Our study has some limitations: for example, we assigned mobbing behaviour at the species level, assessing the most aggressive or vocal individual, and thus individual-level variation cannot be determined. Further, we used models of one owl species, the collared owlet, which is the smallest owl species in Asia. Results may be specific to this species, and this forest, in which it is the most common bird-eating species. Nonetheless, studies of mobbing are relatively rare in Asia (see also Hua et al., 2016), specifically in the investigation of the relationship between functional traits and mobbing behaviours. Consideration of a wide range of potential functional traits is also needed for more synthetic understanding, and thus we discuss each considered trait below, one at a time.

4.1. The effect of sociality

One of the major hypotheses for the formation of mixed-species flocks (MSFs) is to reduce predation risk (Sridhar et al., 2009; Goodale et al., 2017). Predation is reduced in multiple ways: through diluting risk by having many individuals present, by having many eyes to detect a predator, and by birds making alarm calls (Beauchamp, 2014). In our study region, MSFs constitute a significant component of the forest bird community (Jiang et al., 2020), regularly consisting of more than 20 individuals (Jiang, 2007; Zhou et al., 2019) and occasionally reaching up to a size of 100 birds (personal observation & Chen & Hsieh, 2002). MSFs thus result in a variable distribution of birds in time and space in our study system: bird encounter is 'hit-or-miss' depending on whether an MSF is around or not, and this same phenomenon should reduce encounters with the predator. Hence, species that spend most of their time in MSFs were not as available to respond to a mobbing stimulus as other species, even if they are common. In addition, our personal experience obtained when doing similar playbacks of owlets and model presentations in MSFs (Jiang et al., 2020) suggests that when inside MSFs, birds have lessened interest in mobbing. Even though playbacks occasionally attracted members of MSFs to visit, they generally came with low intensity and the whole MSF left shortly thereafter. Given our general results that species more at risk of predation are more active mobbers (see discussion of body size, below), the connection between being protected as an MSF participant and having lower mobbing prevalence makes sense.

Interspecific sociality could also facilitate interspecific recognition (Magrath et al., 2015; Szymkowiak, 2021) and could shape the way that species use social information, consequently affecting mobbing vocalness. We found that species with a higher degree of interspecific sociality tended to exhibit weak vocalness, which suggests that some flocking species reduce their predation risk by acting passively and taking advantage of other species' aggressiveness and vocalness. For instance, Jiang et al. (2020) found that the David's fulvetta is a nuclear species of the flock system in southern China, and that they make long-lasting mobbing calls and had more individuals involved in mobbing than most other mobbing participants. Other 570

species therefore could take advantage of such vocal and aggressive species to reduce their vocalizations, and thereby reduce the probability they might be attacked by predators (Contreras & Sieving, 2011).

We did not find any effect of intraspecific gregariousness, which ran contrary to our hypothesis that the presence of mates or kin in flocks would influence mobbing behaviour. Our result, however, is partially consistent with Cunha et al. (2017b): they found that species in flocks or stable groups tended to mob more, but the kind of group (non-family, family, or cooperative breeders) did not influence mobbing. In other studies, potential mates in flocks increased male mobbing at the community level (Cunha et al., 2017a), and kinship increased mobbing in a one-species study (Griesser & Ekman, 2005). These factors may, however, be very sensitive to seasonality, and some of the playback experiments were conducted during the non-breeding season, which may not have been the best time for males to signal quality to potential breeding partners (Carlson & Griesser, 2021). Gregariousness might also increase mobbing due to simply having more individuals present to mob. But we found that gregariousness did not guarantee mobbing behaviour by multiple individuals: multiple individuals of a species were involved in only 58.4% of all trials. Further work understanding mobbing behaviour at the individual level in these flocks would be worthwhile.

4.2. Other functional traits: body size and foraging strata

Small prey generally have higher mobbing prevalence (Hua et al., 2016; de Lima et al., 2018), and indeed we detected a negative impact of body mass on mobbing prevalence. Previous research suggested that small predators have a strong preference for smaller-sized prey, in part for ease of prey handling and processing (Barnes et al., 2010; Dutour et al., 2017b). The predator our study simulated to elicit mobbing was the collared owlet, which, at about 15 cm in body length and 50 g in body weight, is the smallest owl in Asia, and unlikely to hunt large prey, although unfortunately detailed data on its prey are not available. The smallest species responding to our mobbing trials, such as the fork-tailed sunbird (*Aethopyga christinae*) and yellow-bellied warbler (*Abroscopus superciliaris*), had the highest mobbing frequencies despite relatively low abundance (Table 1). In contrast, large species such as the puff-throated bulbul (*Alophoixus pallidus*) and red-whiskered bulbul (*Pycnonotus jocosus*) were rarely involved in mobbing, although they had relatively high abundance (Table 1).

The impacts of body mass on mobbing behaviour were not limited to mobbing prevalence, as we also found that smaller prey had higher mobbing aggression and vocalness. One explanation is that compared to large prey, small prey are less effective at imposing stress on the predator and altering its behaviour (Consla et al., 2012). For instance, Flasskamp (1994) found that mobbing by the common blackbird (Turdus merula) successfully drove off a small-sized owl (the little owl Athene noctua), but it barely affected a large-sized owl (the tawny owl *Strix aluco*). Therefore, small species likely have to make a greater investment in mobbing to 'move on' predators. An alternative explanation is that mobbing intensity is related to predation risk, and in turn higher predation risk provokes stronger mobbing intensity (Strnad et al., 2012; Dutour et al., 2016; Cunha et al., 2017b). For instance, Motta-Junior & Santos-Filho (2012) found that Neotropical birds mobbed the striped owl (Asio stygius) more intensely than the barn owl (Tyto *alba*), because the former species imposed more threat than the latter one. Less effective aggression and higher vulnerability could jointly motivate the mobbing behaviours of small prey, requiring them to exhibit conspicuous displays to achieve effective mobbing, including the recruitment of other mobbing species.

We did not find any influence on foraging strata on mobbing, similar to Cunha et al. (2017b) and de Lima et al. (2018). One factor that may influence these results is that the forest we worked in was relatively invariant in its structure; in a study that did find significant impact of foraging strata, the researchers sampled a gradient of logging along which the structure of the forest changed substantially (Hua et al., 2016).

4.3. Conclusions

Our study revealed that functional traits have a strong influence on the mobbing behaviours of a diverse bird community in southern China. Species with small body mass, high abundance and low frequency of flocking with heterospecifics had stronger mobbing behaviours in terms of prevalence, aggressiveness and vocal willingness. Our work confirms that both mobbing and flocking are adaptations to predation (Zhou et al., 2021), and it is important to conserve the flocking system and its keystone species that provide anti-predation information (Zou et al., 2018), such as David's fulvetta in this system.

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