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Master Thesis

台灣燕雀目鳥類對鵂鶹(*Glaucidium brodiei)*的群聚滋擾反應

The Mobbing Behavior of Passerine Birds to Collared Owlet (*Glaucidium brodiei*) in Taiwan

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摘要

當獵物面臨捕食風險，獵物往往需要抵抗掠食者來提高自己存活的機率。在燕雀目鳥類群聚中，鳥類會聚集起來發出警戒聲，靠近掠食者，甚至直接攻擊掠食者，這樣的行為稱為群聚滋擾。然而，目前我們並不清楚捕食者在不同季節上食性的改變如何影響小型燕雀目鳥類的群聚滋擾反應。也不了解可能參與群聚滋擾群體的鳥類有什麼樣的生態特徵。我們利用經常捕食小型燕雀目的鵂鶹 (*Glaucidium brodiei*)的叫聲進行回播實驗，模擬掠食者的出現。我們設立的 93 個樣區，並且分別於鳥類的繁殖季(2017 年五月至六月)與非繁殖季(2017 年十二月及 2018 年一月)於每一個樣區各進行一次調查。我們在 9 分鐘的回播實驗中（6 分鐘靜默以 3 分鐘回撥）記錄了每一隻鳥在每一次實驗中是否發出警戒聲以及是否靠近喇叭。結果發現不同季節之間鳥類發出警戒聲的機率並沒有差異(30.88% vs. 29.15%)，然而繁殖季中，鳥類靠近喇叭的機率顯著的高於非繁殖季(25.63% vs. 13.28%)。在兩個海拔段中冠層活動者較底層活動者有較高的機率進行群聚滋擾行為，在低海拔段中體型較小的鳥類有較高的機率靠近喇叭，但中海拔段中體型與靠近喇叭的機率並沒有顯著的相關。我們的結果顯示在不同的季節之間燕雀目鳥類採取了不同的策略，也顯示了參與群聚滋擾反應鳥類的生態特徵。鵂鶹在非繁殖季的食性會從繁殖季的昆蟲為主改變成以鳥類為主，我們推測燕雀目鳥類可能是因為這個原因而在非繁殖季採取較安全的方式來抵抗掠食者。

關鍵字：群聚滋擾、抵抗掠食者、捕食風險、燕雀目鳥類、鵂鶹 (*Glaucidium brodiei*)

Abstract

When prey species face risk of predation, most preys make considerable effort to fight against predators including making alarm call and/or approaching to harass predators. Animal may adjust their anti-predator behavior by evaluating benefits and costs. However, less is known about how prey expresses anti-predator behavior across seasons when these behaviors may be driven by breeding status or shift in predator diet. Moreover, we assessed the influences of ecological traits on mobbing response in passerine community in Taiwan. We conducted 9-minute point count surveys (6-mintue quiet period and subsequent 3-minute playback) of passerine birds with call of Collared Owlet *Glaucidium brodiei*, a diurnal owl that preys on passerines, at 93 sites in breeding season (May and June 2017) and nonbreeding season (December 2017 and January 2018) in Taiwan. We recorded whether the small passerine birds approach and make alarm call or not to evaluate mobbing response. We found that season did not influence probability of making alarm call (30.88% and 29.15% in breeding and nonbreeding season, respectively). However, the probability of approaching was higher in breeding (25.63%) than in nonbreeding season (13.28%). In both elevations, the probability of approaching was significantly higher for canopy species than understory species. We found that species with smaller body mass mobbed more frequently than their larger body mass counterparts in low elevation but not in intermediate elevation. Our findings supported that mobbing responses were different between seasons at community level. We demonstrated the ecological traits of potential mobbers. Furthermore, Collared Owlet has a higher propensity of diet for birds in nonbreeding than in breeding season. It revealed that small passerine birds mob in both seasons but choose a safer way to against predators in season with higher risk.

Key words: Mobbing, Antipredator, Predation risk, Passerine community, Collared Owlet *Glaucidium brodiei*

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從對鳥類完全不懂，到現在寫了一篇鳥類學研究，前前後後花了幾乎6年的時間。在這期間培養了許多能力，例如鳥類辨識、統計分析、邏輯思考、資料處裡以及寫作等，也培養了賞鳥這個能陪伴一生的興趣。非常感謝一路上的夥伴，特別感謝老師對研究生們的用心，全力支持一個跟研究室計畫方向完全摸不著關係的題目。資料收集感謝老師、同學跟學弟妹們幫忙出差。統計分析的方面邱博幫我一起思考了許多問題，提供我非常正確的方向。最感謝的是蔡老師要忍著血壓改幾十頁很破的英文。感謝大家。

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Introduction

Risk of predation is one of the principal causes driving the trade-off of animal behavior and also a selective force in evolution (Lima and Dill 1990). Animals have to balance between predation and other behaviors, such as starvation (Bachman 1993, Houston et al. 1993, Inger et al. 2006) and reproduction (Brown and Shine 2004, Bērziņš et al. 2010). Mobbing behavior benefits preys by approaching and driving the predators away to reduce the risk of predation (move-on hypothesis) (Pettifor 1990, Flasskamp 1994, Pavey and Smyth 1998, Betts et al. 2005). However, mobbing behavior costs prey considerable time and energy (Collias and Collias 1978, Bērziņš et al. 2010) and can even bring the lethal risk (Denson 1979, Motta-Junior 2007). Nevertheless, for most animals, be able to evaluate the risk of predation and allocate the time of anti-predator and other behaviors is the key to survive. In this study, we discussed two ideas of mobbing response: (1) to evaluate engagement of two types of mobbing behaviors across seasons and (2) how ecological traits influence mobbing response by small passerine bird.

Seasonal variation of mobbing response

Generally, making alarm calls and approaching predator are the most common mobbing responses carried out by passerine birds (Curio et al. 1978a). However, these two behaviors represent different functions and exert different pressures upon birds. A large number of studies investigated the function of alarm calls, such as recruiting partners for rebelling against predators (Krams et al. 2008, Krams et al. 2009) and encoding the risk of predators (Templeton et al. 2005). Alarm calls can also attract a mightier predator to drive the predator away (Curio et al. 1978b). For example, the mobbing calls of Light-vented Bulbul *Pycnonotus sinensis* to Collared Scops-owl *Otus lettia* can enhance the probability of Accipitridae raptors attacking the stuffed owls in Taiwan (Fang 2017). A study even revealed that predators only attacked silent dummy individuals but not the calling individuals, which suggested that making alarm calls may have some safety benefits (Kareksela et al. 2013). However, making alarm calls still bring mobbers cost. For example, the nest predators can locate the passerine nests via mobbing calls which results in breeding failure (Krama and Krams 2004).

On the other hand, approaching is also an anti-predator behavior in mobbing response with different strategy. Passerine birds harass or even physically attack potential predators for repelling them. Driving predators away reduce the immediate and future risk of predation. Several previous studies revealed that passerine birds took a high risk by mobbing a dangerous predator, which causes the predators abandoned their roosting site (Flasskamp 1994) and thus benefits with decreasing chance of being preyed (Pavey and Smyth 1998). However, approaching predator could be a fatal behavior as predator could kill prey during mobbing (Denson 1979, Motta-Junior 2007). Furthermore, when male birds are approaching their predator, they must leave their mate, facing the potential problem of cuckoldry (Bērziņš et al. 2010).

Both making alarm calls and approaching bring mobbers costs and benefits. Making alarm calls is the trade-off between self-safety and the risk of nest predation while approaching predator is between reducing immediate risk of predation and death. Approaching should be regarded as a more extreme and dangerous but more effective behavior than making alarm calls because of the fatal risk. Nevertheless, most studies treat the approaching events as the criterion to evaluate the mobbing response but often neglect the alarm calls (Sandoval and Wilson 2012, Tilgar and Moks 2015, Dutour et al. 2016, Dutour et al. 2017). Therefore, understanding the pattern of making alarm call, a less-risk behavior, may also shed light on anti-predator behavior in mobbing passerine community.

The change of environmental condition in regard to seasonality dominates the variation of animal behaviors (Hill 1997), including mobbing behaviors (Shedd 1982). Previous studies indicated that mobbing is often most intense during the breeding season (Shedd 1982, Shimazaki et al. 2017), and it can be attributed to breeding activities such as defending territories and nests (Shedd 1982, Gehlbach and Leverett 1995) or guiding offspring (Griesser and Suzuki 2017). Moreover, studies showed that the predator diet varies between seasons (Silva-Porto and Cerqueira 1990, Tome 1994, Bose and Guidali 2001), and the diet of predator decide the risk predation (Dutour et al. 2017) hence the mobbing response. However, less is known about whether this seasonal pattern of mobbing behavior holds or not concerning different levels of risk.

Ecological traits predict mobbing response

Mobbing behavior is a frequently expressed anti-predator response of small passerine birds when they are facing their potential predator. However, not all species participate in mobbing in a given passerine community when a predator is present (da Cunha et al. 2017, Dutour et al. 2017, Lima et al. 2018). The aspect of why some species are frequent mobbers while others are not is still unclear, especially in Taiwan. The risk of predation should be the driver of this aspect. Dutour et al (2017) indicated that mobbing response of passerine birds increases with the prevalence in predator diet. This study revealed that only the species facing risk of predation express mobbing response. Thus, only potential prey engages in mobbing.

Here, we assessed how the ecological traits are related to mobbing participation. First, body size of prey can be the criterion for the risk of predation as predator only preys on given body size preys (Valcu et al. 2014). We hypothesized that only the species with certain range of body size that is available for predator would participate in mobbing. Second, as the niche overlapping between passerine birds and predator increases, the mobbing response should increase. We hypothesized that prey sharing same space with potential predator are more likely to encounter with predator, resulting in higher risk of predation on prey. So these prey species are more willing to mob their potential predator.

Owls in the genus *Glaucidium* are particularly suitable predator cue to study mobbing behavior in passerine communities due to the bird-preferred diet (Jiménez and Jaksić 1989, Carrera et al. 2008). The mobbing behaviors to most *Glaucidium* species have been well documented. For example, the Eurasian Pygmy Owl *G. passerinum* distributed over coniferous forest in Eurasia is mobbed by small passerine bird species such as parus-like birds or Goldcrest *Regulus regulus* and Common Firecrest *R. ignicapilla* (Zimmermann and Curio 1988, Dutour et al. 2016, Dutour et al. 2017). The Ferruginous Pygmy Owl *G. brasilianum* in tropical forest in Brazil is also mobbed by diverse species of small passerine (Sandoval and Wilson 2012, Tilgar and Moks 2015, Cunha et al. 2017). In contrast to other species in this genus, less is known about the mobbing behavior of passerine communities to Collared Owlet *G. brodiel*, an oriental and small owl species only 60-78g (Tseng and Lin 2010), especially in Taiwan. Furthermore, Collared Owlet has a seasonal variation in diet (Lin. personal communication) and how the changing diet in different seasons influence the mobbing behavior is unclear.

In this study, we treated the call of Collared Owlet as the predator cue and examined whether the small passerine communities adapt different strategies of mobbing according to season. Here, we predicted that the different intensity of mobbing responses will be expressed in passerine communities between breeding and non-breeding season. Specifically, the approaching behavior, a higher risk behavior, would happen more frequently in breeding season than in nonbreeding season. However, we expected that the likelihood of making alarm calls should be similar in both seasons. Moreover, the smaller species would mob more frequently than the larger body , and canopy layer species would mob the most because they face higher rate of being killed by Collared Owlet.

Methods

The study was conducted in several areas in central and eastern Taiwan. All sites were located in areas with confirmed distribution of Collared Owlet based on eBird database and/or previous personal observations. We established 45 and 48 sites in low elevation (200-1000m) and intermediate elevation (1200-2800m), respectively, and all sites were at least 500m apart to avoid an individual contributing more than one response to analyses. The study sites in low elevation were located in Chiayi County (23°20'N 120°35E), Nantou County (23°55'N 120°53'E) and Hualien County (23°18'N 121°15'E), while sites in intermediate elevation were located in Chiayi County (23°29'N 120°46'E). All sites were dominated by secondary broad-leaved forest and some sites in intermediate elevation are mixed with Japanese Cedar *Cryptomeria japonica* plantation. We avoided the pure monoculture planation forests because these forests typically have sparse and monotonous vertical foliage structure (Lee et al. 2006) and may affect the movement of forest birds (Gillies et al. 2011, Shimazaki et al. 2017).

We conducted experiments at both low and intermediate elevation sites in breeding season (late April to early June 2017) and nonbreeding season (December 2017 to January 2018), and broadcasted Collared Owlet calls as the acoustic cues. We placed a loudspeaker on the ground and one to two observers stood 10m from the loudspeaker in different directions to observe the behavior of small passerine birds. In each site, we conducted a silent survey at first six minutes following by a three minutes playback experiment. During the first six minutes, all the bird individuals that we saw or heard were identified and counted, and were treated as potential mobbers. Observers also noted the distance and direction of all bird individuals before birds received the acoustic cues. During the following three minutes playback experiment, we quantified alarm call response by detecting whether there was a violent acoustic transformation of birds. The approach response was quantified when the birds approached within a 10m radius of the loudspeaker after birds received the acoustic cues. The individuals that were observed within 10m radius around the loudspeaker during the silent period were excluded from analyses because we could not confirm that whether the approaching behavior was the response to the playback or not. But if these birds made alarm calls, we still treated as the responses of making alarm calls. If a same bird species moved as a pair or a group, we treated as an individual to avoid the potential problem of pseudoreplication. Additionally, we excluded the migratory species and winter visitors from analysis so the comparisons between seasons have similar community base. Calling and approaching responses were binary variables. An individual that approached within 10m from loudspeaker or made an alarm call in three minutes playback experiment was recorded as ”1” while an individual that did not approach within 10m from loudspeaker or did not change their call type was recorded as “0”. All experiments were conducted within five hours after sunrise as it is the time of the day birds had the highest activity. No experiment was carried out in rainy and/or windy day. If Collared Owlet were recorded during playback experiment, we treated that experiment as invalid. The presence of Collared Owlet might influence the willingness to mob our playback.

We obtained the body mass from Hsu (2016) and Severinghaus et al. (2012). The activity layers were categorized according to the description from the field guide of wild bird in Taiwan (Hsiao and Li 2017). The prey species were categorized into (1) understory: moving on the ground or moving in the dense bush, (2) canopy: moving on the top 2/3 layer of a tree (see Appendix 1).

We broadcasted playback via a loudspeaker (HANLIN-M53 Taiwan) inserted a micro SD memory card with the acoustic files of owlet call. We adjusted the amplitude level to the maximum value of the loudspeaker during the experiment and it was matched the natural calls of Collared Owlet. All the trials were conducted with the same amplitude level.

To test the hypothesis of season variation in mobbing response, we evaluated whether the probability of making alarm calls and approaching were influenced by season and elevation using logistic linear mixed model. Models for making alarm call and approaching were run separately. Study area and species were introduced as the random effects in both models. Season (breeding and nonbreeding season), elevation (low and intermediate elevation) and the interaction between season and elevation were the explanatory factors in the fixed part of both two models. Then, to test the hypothesis of ecological traits in relation to mobbing response, we only used data in breeding season. We evaluated how probability of approaching was influenced by body mass and activity layers using logistic linear mixed model. Study area (We had 11 areas and each area include 6 to 14 sites. In one single day, we only finished sites in one area. See Figure 1.) and species were introduced as the random effects in the models. Body mass (log) and activity layer (understory, and canopy) were the explanatory factors in the fixed part. We ran models twice on intermediate and low elevation communities separately. All analyses were conducted using the package lme4 in the software R (R Core Team 2018).

Results

We conducted 148 rounds of playback experiments and observed 747 individuals during our study. In breeding season, we observed 31 species during our study and we recorded 22 species with at least one individual mobbed to the Collared Owlet. In nonbreeding season, we observed 32 species during our study and we recorded 22 species that mobbed to the Collared Owlet. On average, 5.88±3.44 individuals were observed and 2.77±1.57 mobbed in each site during breeding season. 4.04±2.65 individuals were observed and 1.87±1.19 mobbed in each site during nonbreeding season.

Seasonal variation of mobbing response

We recorded 476 individuals in breeding season, of which 147 individuals made alarm call (proportion of making alarm call = 30.88%) and 122 individuals approached the loudspeaker within a 10m radius (proportion of approach = 25.63%). We recorded 271 individuals in nonbreeding season, of which 79 individuals made alarm call (proportion of making alarm call = 29.15%) and 36 individuals approached the loudspeaker within a 10m radius (proportion of approach = 13.28%). Small passerine birds had similar likelihoods of making alarm call in both breeding season (Figure 2) and nonbreeding season as season was not a significant factor in influencing the probability of making alarm call (Table 1). However, they were less likely to approach the loudspeaker in the nonbreeding season (Figure 3). The probability of approaching was significantly lower in nonbreeding season than in breeding season (Table 2). Furthermore, the pattern of mobbing did not vary between elevation ranges in community level.

Ecological traits predict mobbing response

The passerine birds that were smaller in body sizes and inhabit in subcanopy were the main participants in mobbing community. Morrison's Fulvetta *Alcippe morrisonia* was the most dominant species participating in mobbing activity in our experiments in both elevation levels and seasons (Table 3, 4). White-bellied Erpornis *Erpornis zantholeuca* and Black-naped Monarch *Hypothymis azurea* were the second and third most abundance species, respectively, that mobbed in low elevation area (Table 3), while Taiwan Yuhina *Yuhina brunneiceps* and Rufous-faced Warbler *Abroscopus albogularis* were also participated actively in intermediate elevation area (Table 4).

In low elevation area, the body mass was negatively related to the probability of approaching (Table 5) but not in intermediate elevation area (Table 6). In both elevation area, the canopy species had significantly higher probability of approaching than understory species. (Table 5 and Figure 4, 5).

Discussions

Our playback experiment demonstrated that the mobbing strategies in passerine community were different across seasons in Taiwan. Small passerine birds made alarm calls with similar percentage in both seasons but approached predator cue less in nonbreeding season compared to breeding season. The species that are potential prey are the main members in mobbing community. These results support our hypotheses and suggested that the small passerine birds expressed a more radical anti-predator behavior in breeding season compared to nonbreeding season.

Seasonal variation of mobbing response

Our findings showed stronger mobbing response during breeding season than non-breeding season, which agreed with most of the previous mobbing studies (Root 1969, Shedd 1982, 1983, Zimmermann and Curio 1988, Shimazaki et al. 2017). Most studies attributed the seasonal variation of mobbing behavior to the needs of reproduction and other breeding related activities. From the physiological perspective, the higher testosterone concentration in breeding season regulate the breeding behavior such as display (da Cunha et al. 2017), incubation condition (Balthazart 1983, De Jong et al. 2016), competition for female, and defending territory (Wingfield et al. 1987). The testosterone may also contribute to the aggressive anti-predator behavior. The offspring may learn how to response to predators from the mobbing activity of breeders and they were more likely to become breeders in the subsequence season (Griesser and Suzuki 2017). On the other hand, in a study in Brazil where passerine birds consolidate year-round territories, the researchers found no differences in mobbing response across seasons (Cunha et al. 2017). To sum up, the breeding status of passerine is the one of the important factors driving the anti-predator behaviors.

In addition to breeding status, a more traditional approach in explaining intensity of mobbing behavior, predator diet may also affect the mobbing behavior (Dutour et al. 2016, Dutour et al. 2017). In Dutour's studies, it showed that mobbing intensity was associated with its prevalence in predator diet. When the species were preyed more often, the more aggressive mobbing response was expressed. Another studied showed that the predator with the higher bird-prevalence diet, suffered a higher intensity of being mobbed. In our opinion, this idea might be applied to the explanation in seasonal mobbing response. Studies have shown that many owl species express seasonal variation in diet (Korpimäki 1986). The season-changing diet of owls in genus *Glaucidium* are no exception, and the diet during non-breeding season is passerine-prevalence (Mikkola 1983, Solheim 1984). We argue that this might be the key driver in explaining the different mobbing responses across season in Taiwan. Tseng and Lin (2012) found that insect is the most important diet of Collared Owlet in breeding season, following by amphibian and reptile (Tseng and Lin 2012). However, during the non-breeding season the diet of Owlet was mostly consisted of small passerine birds (W.L. Lin, personal communication). The change of diet makes Owlet an extremely dangerous predator for the passerine during nonbreeding season. Our results showed that the small passerines use both approaching and making alarm call while responding to predator cue in breeding season. However, the passerines were less likely to approach in nonbreeding season than in breeding season, suggesting that the passerine community still mobbed but with a safer strategy when facing the extremely dangerous predator during non-breeding season.

The probability of making alarm calls and approaching did not differ between communities from two ranges of elevation as neither the main effects nor interaction term was significant. This result revealed that despite of the differences of community composition between elevations (Table1, 2), our predator stimulation can give rise to similar mobbing behaviors. The non-significant results may be explained by two possible reasons: first, our result indicated that Morrison's Fulvetta was the main mobber responding to the call of Collared Owlet in both elevation levels. Morrison's Fulvetta is a common species distributed across broad elevation range from lowlands to mountains. Thus, the domination of mobbing might be the one of reason explaining non-significant results between elevation levels. Furthermore, Morrison's Fulvetta is a small passerine (13-14 cm body length) mainly active in the subcanopy level of the forest. These ecological traits make it suffer higher risk of predation from owls in the genus *Glaucidium* is the predator (Cunha et al. 2017, Lima et al. 2018). Therefore, the Morrison's Fulvetta responded most strongly in our study with Collared Owlet as our cue of predator. Second, some species move altitudinally between these two elevation ranges between seasons. In non-breeding season the distribution of some species such as Taiwan Yuhina shifted downward. Therefore, the bird community in low elevation area may be mixed with the community in intermediate elevation range during nonbreeding season. Taiwan Yuhina, a common and dominant species widely distributed in intermediate elevation areas, were never recorded in the low elevation study areas during breeding season, but were recorded eight times in low elevation study areas during nonbreeding season. Thus, the similar mobbing responses between communities from two elevation ranges might be similar.

Most studies focus on whether preys approach their predators as a criterion for mobbing response (Sandoval and Wilson 2012, Tilgar and Moks 2015, Dutour et al. 2016, Dutour et al. 2017). However, alarm call is also an important strategy to reduce the risk of predation (Kareksela et al. 2013). Indeed, treating this calling behavior as criterion in mobbing investigation could be problematic due to detection issue. Sandoval and Wilson (2012) and Dutour et al (2017) noted that it was not possible to ensure which bird is calling or not. Also, acoustic survey may loss species when richness is high (Haselmayer and Quinn 2000). However, we thought it is still possible to ensure birds calling or not when the numbers of individuals in our playback experiments were relatively small (5.03±3.23 individuals recorded per site on average). Our results revealed that alarm calls would be the low-risk strategy. We argued that future studies should consider the alarm calls as well as approaching behavior in mobbing response to obtain more information of mobbing motivation.

Ecological traits predict mobbing response

Our study revealed that not all species respond to predator stimulation equally. The lighter and canopy species were more likely to mob than other species. The main species participating in mobbing were all the small-sized birds. The body mass of all mobbing species were lighter than 100g. The body mass of five species mainly participating in mobbing in both elevation level were even lighter than 20g (Appendix 1), and it indicated that smaller birds might face a higher risk of predation. Although, the detailed diet of Collared Owlet is still unclear, based on data from other species in the genus *Glaucidium*, small passerine birds were the most common prey (Carrera et al. 2008). Collared Owlet could exert pressure on species with the similar ecological trait.

Our results supported that canopy species mobbed more frequently than understory species. Collared Owlet is a predator often perches on the branches in the dense forest (Hsiao and Li. 2017). Thus, the canopy species of the forest should be the potential prey and they experience the higher risk of predation than understory species. Our results didn't agree the previous study by Cunha (2018). In Cunha's (2018) study, passerine birds were categorized in into three foraging layers, understory, groud-living and canopy. Their result indicated that canopy and understory species mob more frequently than ground-living species. Our results did not agree with their results. The owl models they used in their study attack prey with a top-down strike, thus the understory species are easily to become target and under the high risk of predation. In our study, in other words, our understory species are "shrub-living" species. the species which we defined as the understory species prefer the dense understory plantation. We thought the dense plantation is the shelter for understory species from the predation of the Collared Owlet. The results also did not agree with the prediction of body mass effect on mobbing response in intermediate elevation area. The insignificant results may due to the smaller range in body size of intermediate elevation community (5.9g to 47.9g) as compared to the range in body size of lowelevation community (from 5.9g to 89.9g). Thus, this may hide the trends of mobbing response in this community.

Conclusion

Ultimately, the breeding status as a driver on seasonal variation of mobbing behavior is widely discussed. According to the dietary prevalence of Collared Owlet and how passerine birds adjust the strategy of mobbing, we suggested that the season-changing diet prevalence of predators should be a strong factor influencing the mobbing response in Taiwan. However, we did not suggest that predator diet is the only driver and the influence of breeding status may as well play an important role in explaining the difference of mobbing response across season. Future studies with suitable experimental design are needed to elucidate how these factors shape the behavioral response.

Mobbing is a risky behavior. If animals fail in mobbing, they could cause death. They have to assess the risk to response to predation. Only when the benefits are larger than costs, animals would engage in anti-predator behavior. Our results showed that the benefits brought by mobbing behavior are higher than costs in the species facing the risk of predation. To sum up, the mobbing behavior is the key of releasing the predation pressure for potential preys.

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Table

Table 1. Effect of season, elevation and the interaction of season and elevation on the probability of passerine communities making alarm calls during playback experiment using logistic linear mixed model.

Parameter	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	-1.17	0.39	-2.94	0.002**
Season (breeding v.s. nonbreeding)	-0.06	0.31	-0.19	0.85
Elevation (intermediate v.s. low)	-0.36	0.41	-0.85	0.40
Season × Elevation	-0.28	0.43	-0.65	0.52

*** <0.001, ** <0.01, * <0.05.

Table 2. Effect of season, elevation and the interaction of season and elevation on the probability of passerine communities approaching during playback experiment using logistic linear mixed model.

Parameter	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-1.25	0.31	-4.05	< 0.001 ***
Season (breeding v.s. nonbreeding)	**-1.03**	**0.33**	**-3.1**	**0.002 ** **
Elevation (intermediate v.s. low)	-0.4	0.36	-1.13	0.26
Season × Elevation	0.14	0.46	0.31	0.76

*** <0.001, ** <0.01, * <0.05.

Table 3. The number of individuals (participated in mobbing/observed) recorded for each species in playback experiments in breeding and nonbreeding seasons in low elevations. Mobbing activity includes making alarm calls or approaching.

Species	**Common name**	**Breeding**	**Nonbreeding**
Alcippe morrisonia	Morrison’s Fulvetta	29/41	15/21
Erpornis zantholeuca	White-bellied Erpornis	19/25	5/12
Hypothymis azurea	Black-naped Monarch	10/14	2/5
Dicaeum minullum	Plain Flowerpecker	8/12	1/2
Hypsipetes leucocephalus	Black Bulbul	6/22	3/18
Pomatorhinus musicus	Taiwan Scimitar-Babbler	3/19	2/10
Schoeniparus brunneus	Dusky Fulvetta	2/29	0/6
Parus monticolus	Green-backed Tit	2/4	1/2
Dicrurus aeneus	Bronzed Drongo	1/4	0/6
Pericrocotus solaris	Gray-chinned Minivet	1/4	4/8
Dendrocitta formosae	Gray Treepie	1/4	0/4
Cyanoderma ruficeps	Rufous-capped Babbler	1/14	0/13
Liocichla steerii	Steere's Liocichla	1/1	
Heterophasia auricularis	White-eared Sibia	1/2	2/5
Megapomatorhinus erythrocnemis	Black-necklaced Scimitar-Babbler	0/1	
Abroscopus albogularis	Rufous-faced Warbler	0/6	0/2
Psilopogon nuchalis	Taiwan Barbet	0/9	1/13
Cinclidium leucurum	White-tailed Robin	0/5	0/1
Niltava vivida	Vivid Niltava		2/7
Yuhina brunneiceps	Taiwan Yuhina		2/4
Dicaeum ignipectus	Fire-breasted Flowerpecker		1/1
Dendrocopos canicapillus	Gray-capped Woodpecker		0/1
Ficedula hyperythra	Snowy-browed Flycatcher		0/5

Table 4. The number of individuals (participated in mobbing/observed) recorded for each species in playback experiments in breeding and nonbreeding seasons in intermediate elevations. Mobbing activity includes making alarm calls or approaching.

Species	**Common name**	**Breeding**	**Nonbreeding**
Alcippe morrisonia	Morrison's Fulvetta	18/24	7/11
Yuhina brunneiceps	Taiwan Yuhina	15/18	5/7
Heterophasia auricularis	White-eared Sibia	12/42	2/8
Abroscopus albogularis	Rufous-faced Warbler	11/23	5/22
Liocichla steerii	Steere's Liocichla	9/27	5/13
Parus monticoluse	Green-backed Tit	5/6	6/7
Cyanoderma ruficeps	Rufous-capped Babbler	3/18	1/14
Horornis acanthizoides	Yellowish-bellied Bush-Warbler	2/11	1/2
Niltava vivida	Vivid Niltava	2/5	
Cinclidium leucurum	White-tailed Robin	2/19	
Aegithalos concinnus	Black-throated Tit	1/2	3/3
Ficedula hyperythra	Snowy-browed Flycatcher	1/6	0/3
Psilopogon nuchalis	Taiwan Barbet	1/4	
Pomatorhinus musicus	Taiwan Scimitar-Babbler	1/1	0/1
Brachypteryx montana	White-browed Shortwing	1/11	0/5
Dicrurus macrocercus	Black Drongo	0/1	
Periparus ater	Coal Tit	0/5	3/4
Schoeniparus brunneus	Dusky Fulvetta	0/10	0/2
Regulus goodfellowi	Flamecrest	0/4	2/3
Tarsiger johnstoniae	Collared Bush-Robin	0/2	2/5
Fulvetta formosana	Taiwan Fulvetta	0/9	0/1
Pnoepyga formosana	Taiwan Cupwing	0/7	0/8
Actinodura morrisoniana	Taiwan Barwing		1/1
Pericrocotus solaris	Gray-chinned Minivet		1/3
Dicaeum ignipectus	Fire-breasted Flowerpecker		1/2
Megapomatorhinus erythrocnemis	Black-necklaced Scimitar-Babbler		0/1

Table 5. Effect of activity layer, body mass (log) on the probability of passerine communities approach during playback experiment in low elevations using logistic linear mixed model.

Parameter	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	1.17	0.99	1.18	0.24
Body mass (log)	**-0.79**	**0.31**	**-2.59**	**0.01****
Activity layer (canopy v.s. understory)	**-1.73**	**0.52**	**-3.31**	**<0.001*****

*** <0.001, ** <0.01, * <0.05.

Table 6. Effect of activity layer, log body mass on the probability of passerine communities approach during playback experiment in intermediate elevations using logistic linear mixed model.

Parameter	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	-0.47	1.15	-0.41	0.68
Body mass (log)	-0.02	0.39	-0.06	0.95
Activity layer (canopy v.s. understory)	**-1.64**	**0.55**	**-2.97**	**0.002****

*** <0.001, ** <0.01, * <0.05.

Figure

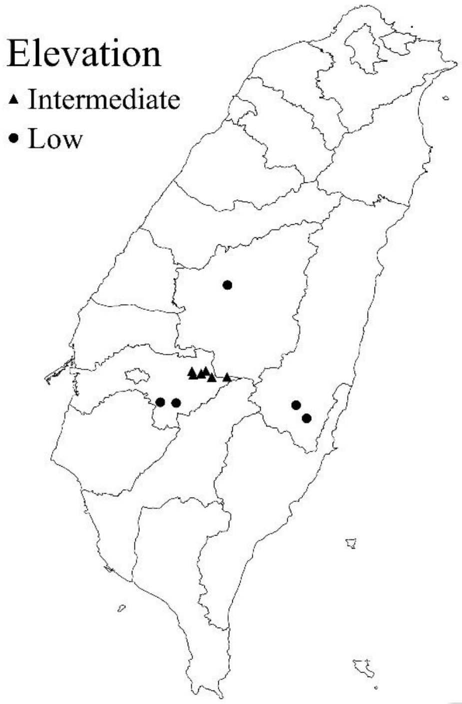

Figure 1. Study area of our playback experiments. Triangle represents the experimental sites in intermediate elevation and these sites were located in Chiayi County. Circle represents the experimental sites in low elevation and these sites were located in Chiayi, Nantou, and Hualien Counties.

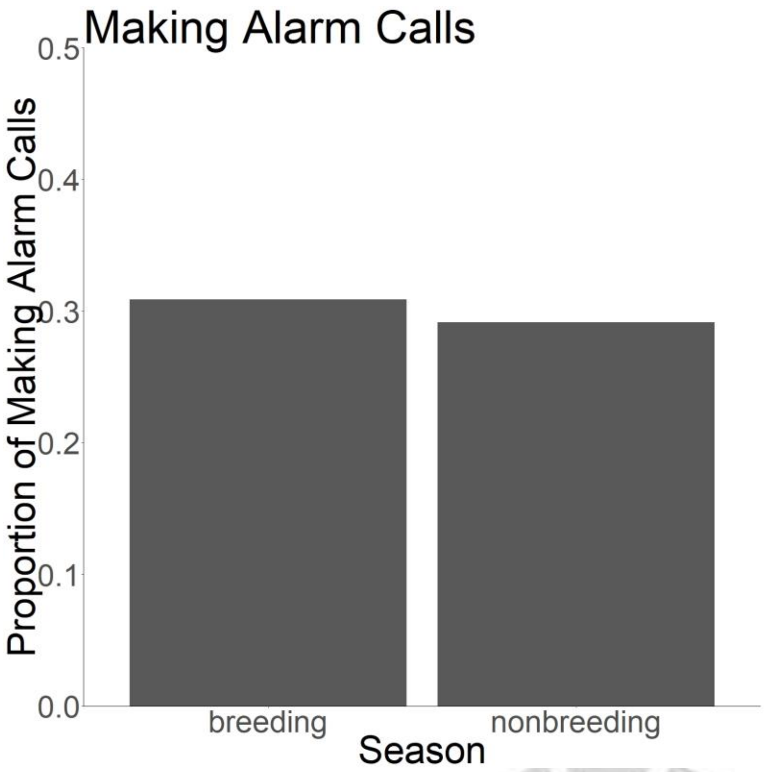

Figure 2. The proportion of individual making alarm calls in breeding season and nonbreeding season.

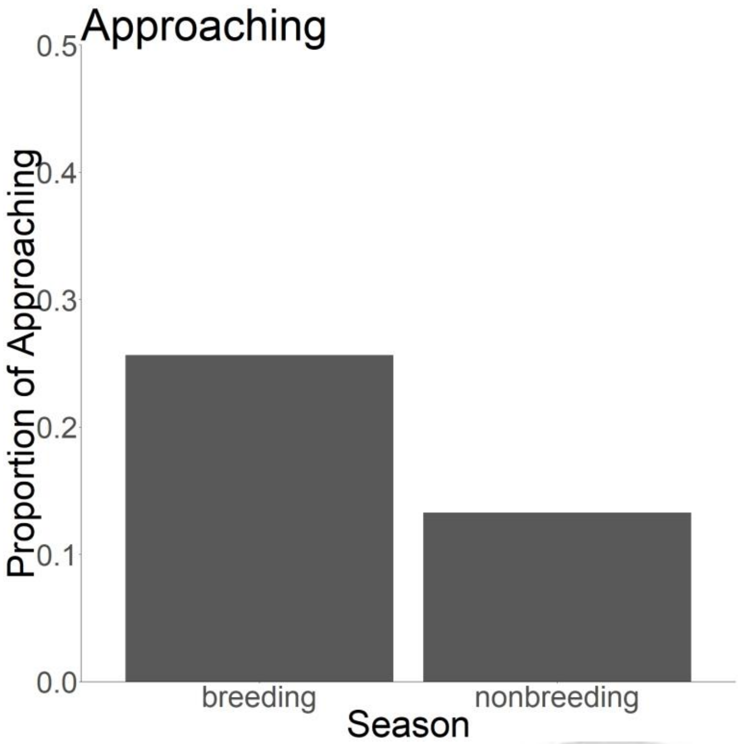

Figure 3. The proportion of individual approaching in breeding season and nonbreeding season.

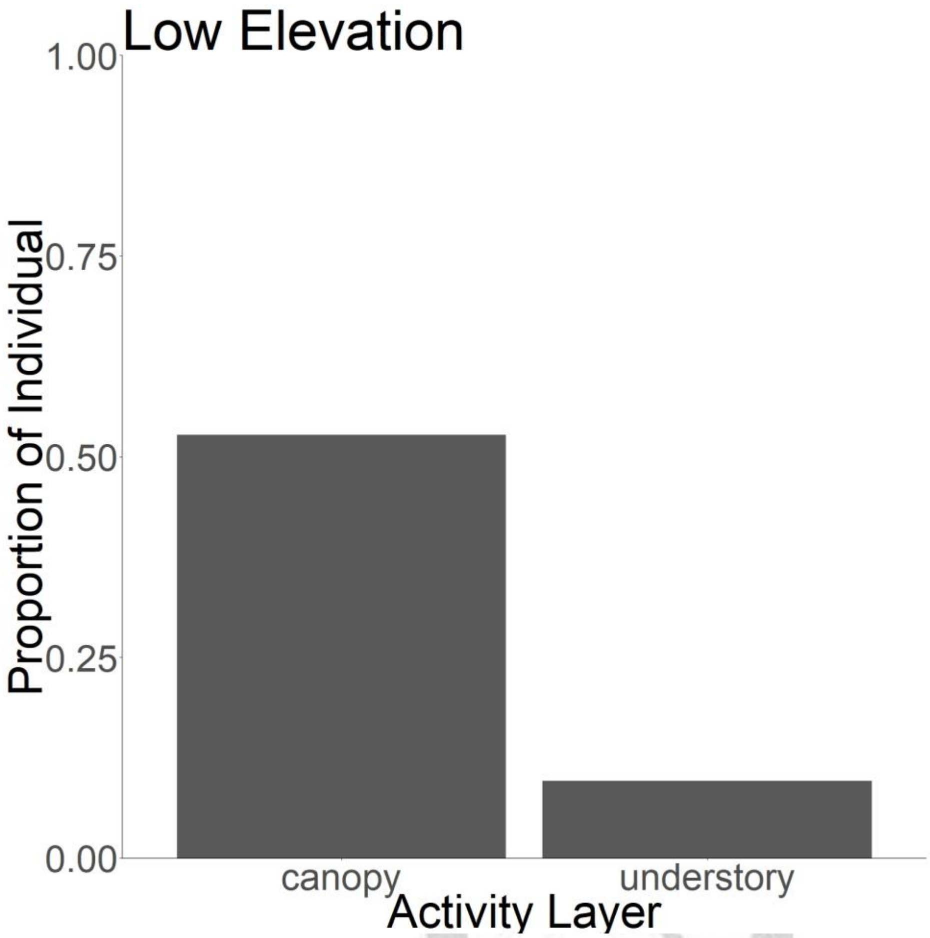

Figure 4. The proportion of individual mobbed in canopy and understory species.

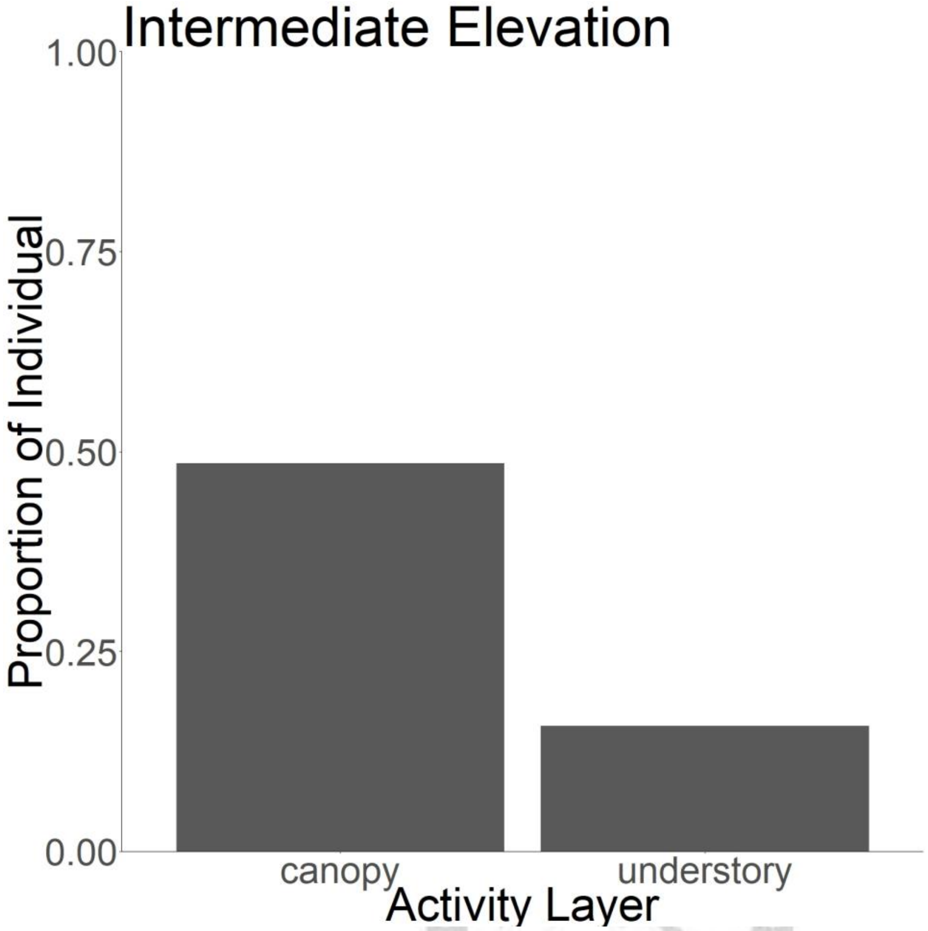

Figure 5. The proportion of individual mobbed in canopy and understory species.

Appendix

Appendix 1. List of all species observed during the survey and their body mass and activity layer (data from Hsu (2016) and Severinghaus et al. (2012)).

Species	**Common name**	**Body mass (g)**	**Activity layer**
Abroscopus albogularis	Rufous-faced Warbler	5.9	canopy
Dicaeum minullum	Plain Flowerpecker	6	canopy
Regulus goodfellowi	Flamecrest	6.2	canopy
Aegithalos concinnus	Black-throated Tit	6.2	canopy
Dicaeum ignipectus	Fire-breasted Flowerpecker	7.5	canopy
Periparus ater	Coal Tit	8.1	canopy
Erpornis zantholeuca	White-bellied Erpornis	11	canopy
Hypothymis azurea	Black-naped Monarch	12.1	canopy
Yuhina brunneiceps	Taiwan Yuhina	12.5	canopy
Parus monticoluse	Green-backed Tit	12.6	canopy
Alcippe morrisonia	Morrison's Fulvetta	13.9	canopy
Pericrocotus solaris	Gray-chinned Minivet	17.9	canopy
Niltava vivida	Vivid Niltava	23.4	canopy
Dendrocopos canicapillus	Gray-capped Woodpecker	30.2	canopy
Actinodura morrisoniana	Taiwan Barwing	32.9	canopy
Dicrurus aeneus	Bronzed Drongo	34.4	canopy
Heterophasia auricularis	White-eared Sibia	47.6	canopy
Hypsipetes leucocephalus	Black Bulbul	49.1	canopy
Dicrurus macrocercus	Black Drongo	57.2	canopy
Psilopogon nuchalis	Taiwan Barbet	78.8	canopy
Dendrocitta formosae	Gray Treepie	89.9	canopy
Horornis acanthizoides	Yellowish-bellied Bush-Warbler	7.2	understory
Ficedula hyperythra	Snowy-browed Flycatcher	9.5	understory
Cyanoderma ruficeps	Rufous-capped Babbler	10.8	understory
Fulvetta formosana	Taiwan Fulvetta	12.5	understory
Tarsiger johnstoniae	Collared Bush-Robin	14.9	understory
Pnoepyga formosana	Taiwan Cupwing	15.5	understory

Appendix 1. (Continued)

Species	**Common name**	**Body mass**	**Activity layer**
Brachypteryx montana	White-browed Shortwing	17.3	understory
Schoeniparus brunneus	Dusky Fulvetta	18.6	understory
Cinclidium leucurum	White-tailed Robin	25.6	understory
Liocichla steerii	Steere's Liocichla	31.6	understory
Pomatorhinus musicus	Taiwan Scimitar-Babbler	38.3	understory
Megapomatorhinus erythrocnemis	Black-necklaced Scimitar-Babbler	67.1	understory