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Seasonal differences in community-level mobbing responses of passerines toward a diurnal owl in Taiwan

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Prey use a variety of anti-predator behavior, including alarm calling and approaching predators, and may adjust these behaviors by evaluating their benefits and costs. However, it remains unclear how prey expresses anti-predator behavior across seasons, when both breeding status or predator diet may influence perceived risk. We conducted nine-minute playback surveys (six-minute quiet period and subsequent three-minute playback) using calls of Collared Owlet (*Glaucidium brodiei*), a diurnal owl that preys on passerines, at 93 sites during breeding season and non-breeding season in Taiwan. We quantified whether the small passerine birds approach and make alarm call or not to quantify mobbing response. We found that probability of making alarm calls did not differ between seasons (30.88% and 29.15% in breeding and non-breeding season, respectively), whereas probability of approaching was higher in breeding (25.63%) than in non-breeding season (13.28%). To verify that responses were specific to predator cues rather than to loud vocalizations in general, we conducted supplementary playbacks using calls of a non-predatory species, Taiwan Barbet (*Psilopogon nuchalis*), which elicited markedly lower mobbing responses. Together, these results indicate that small passerine birds mob in both seasons but reduce the use of higher-risk behaviors against predators during the non-breeding season, consistent with seasonal variation in predation risk.

Keywords: Mobbing, Predation risk, Passerine community, Collared Owlet, Playback experiment

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BACKGROUND

Risk of predation is a major selective force shaping behavior trade-offs and life-history evolution (Lima and Dill 1990). Animals have to balance anti-predator behavior with competing demands such as foraging (Bachman 1993; Houston et al. 1993; Inger et al. 2006) and reproduction (Bērziņš et al. 2010, Brown and Shine 2004). Contemporary frameworks emphasize how prey assess risk dynamically across “landscapes of fear,” adjusting behavior to spatial and temporal variation in perceived danger (Gaynor et al. 2019). Mobbing behavior benefits prey by approaching and driving the predators away to reduce the risk of predation (move-on hypothesis) (Betts et al. 2005; Flasskamp 1994; Pavey and Smyth 1998; Pettifor 1990). However, mobbing behavior is energetically costly (Bērziņš et al. 2010; Collias and Collias 2014) and can expose individuals to injure or even the lethal risk (Denson 1979; Motta-Junior 2007). Because these trade-offs require precise risk assessment, understanding how prey modulate mobbing is central to anti-predator ecology. In this study, we examine mobbing responses of small passerine birds through two common anti-predator behaviors.

Generally, making alarm calls and approaching predators are two widely documented components of mobbing responses in passerine birds (Curio et al. 1978b). These two behaviors represent different functions and exert different pressures upon birds. Alarm calls can recruit partners to collectively repel predators (Krams et al. 2009; Krams et al. 2008) or encoding the level of predation risk (Templeton et al. 2005). Alarm calls may even attract a higher-level predator, thereby displacing the immediate threat (Curio et al. 1978a). For example, the mobbing calls of Light-vented Bulbul (*Pycnonotus sinensis*) toward Collared Scops-owl (*Otus lettia*) can enhance the probability of Accipitridae raptors attacking the stuffed owls in Taiwan (Fang et al. 2020). Some study 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 costs, such as increasing the chance that nest predators locate breeding sites (Krama and Krams 2004). By contrast, approaching predator is a more direct and potentially dangerous anti-predator behavior. Passerines may harass or physically attack potential predators in an attempt to drive them away, thereby reducing the immediate and future risk of predation (Flasskamp 1994; Pavey and Smyth 1998). However, approaching can be fatal as predator could kill prey during mobbing (Denson 1979; Motta-Junior 2007) and may lead to increased risk of cuckoldry if males leave their mates unattended (Bērziņš et al. 2010).

Although mobbing often includes both calling and approaching, fleeing is also a widespread and generally low-risk anti-predator strategy across animal taxa (Caro 2005; Lima and Dill 1990). Because fleeing maximizes immediate survival by increasing distance from the threat, it is frequently favored when individuals are not constrained by defending nests, mates, or fixed resources. However, fleeing does not require individuals to interact with or stay near the predator, and thus cannot be reliably quantified in standardized playback experiments. For these reasons, and because our focus is on behaviors that actively engage with predator cues, we restricted our analyses to alarm calling and approaching, the two primary components of passerine mobbing.

Seasonal changes in environmental conditions also influence animal behaviors (Hill 1997), including mobbing behaviors (Shedd 1982). Most studies indicated that mobbing is most intense during the breeding season (*e.g.*, Krams and Krama 2002, Shedd 1982, Shimazaki et al. 2017), and it can be attributed to breeding activities such as defending territories and nests (Gehlbach and Leverett 1995, Shedd 1982) or guiding offspring (Griesser and Suzuki 2017). However, some studies have documented stronger mobbing in non-breeding season (Dutour et al. 2019), highlighting that seasonal patterns may depend on ecological context. Seasonal variation in predator diet (Bose and Guidali 2001; Silva-Porto and Cerqueira 1990; Tome 1994) may also shape mobbing responses because predation risk is influenced by prey prevalence in predator diets (Dutour et al. 2017). However, despite increasing attention on seasonal risk dynamics, it remains unclear whether different components of mobbing behavior, such as alarm calling versus approaching, exhibit consistent seasonal patterns.

Owls in the genus *Glaucidium* are particularly suitable predator cues for studying passerine mobbing behavior because of their bird-dominated diets, and mobbing responses toward many *Glaucidium* species have been well documented (Carrera et al. 2008; Jiménez and Jaksić 1989). For example, the Eurasian Pygmy Owl (*G. passerinum*) is mobbed by parids, Goldcrest (*Regulus regulus*) and Common Firecrest (*R. ignicapilla*) in coniferous forests (Dutour et al. 2016; Dutour et al. 2017; Zimmermann and Curio 1988). The Ferruginous Pygmy Owl (*G. brasilianum*) in tropical forest is similarly mobbed by diverse species of small passerine (Sandoval and Wilson 2012, Tilgar and Moks 2015). In contrast, mobbing responses toward the Collared Owlet (*G. brodiei*), an oriental species, remain poorly understood, especially in Taiwan. Although anecdotal evidence suggests seasonal shifts in its diet (W.L. Lin, personal communication), the implications of such variations for passerine mobbing behavior are unclear.

In the study, we used the call of Collared Owlet, a small diurnal owl known to evoke strong mobbing reactions from small birds, as the predator cue to examine whether the small passerine communities adapt different strategies of mobbing according to season. We predicted that the mobbing intensity would be expressed in passerine communities between breeding and non-breeding season. Specifically, we expected the higher-risk behavior of approaching to occur more frequently in breeding season than in non-breeding season, whereas the likelihood of making alarm calls would remain similar across seasons. By conducting experiments across two elevation ranges, we also aimed to assess whether community composition influences mobbing expression. Finally, supplementary trials incorporating a non-predatory control call allowed us to confirm that passerine responses were specific to predator cues rather than a generalized reaction to any loud vocal stimulus.

MATERIALS AND METHODS

Study area

Playback experiments were conducted across central Taiwan, encompassing Chiayi and Nantou Counties (23.48-23.91°'N, 120.58-120.88°E) in the west and Hualien County in the east (23.30°N, 121.25°E) (Fig. 1). The study areas were located in the foothill region, characterized by a mosaic of secondary broad-leaved forest, bamboo groves, and mixed hardwood plantation. We avoided the pure monoculture plantation 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 established 45 and 48 sites along the trail 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.

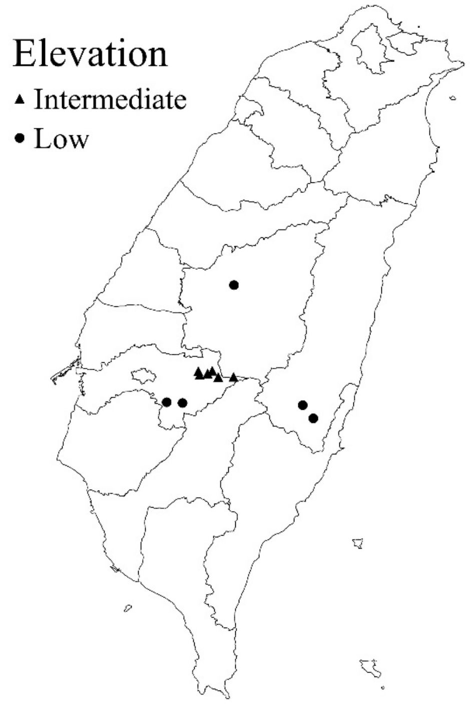

Fig. 1. Study area of playback experiments. Triangle represents the experimental sites in intermediate elevation and these sites were located in Chiayi County. Circle represents the experimental sites in low elevation and these sites were located in Chiayi, Nantou, and Hualien Counties.

Playback experiment design

We evaluated passerine community responses to the Collared Owlet and conducted two stages of experiments. During the first stage, we broadcasted Collared Owlet calls as the acoustic cues in both low- and intermediate-elevation sites from late April to early June 2017 (breeding season) and from December 2017 to January 2018 (non-breeding season). At the second stage, we added additional control trails using the call of Taiwan Barbet (*Psilopogon nuchalis*), a non-predatory frugivore, in 15 of the intermediate-elevation sites in June 2022 (breeding season) and February 2023 (non-breeding season; detailed see below). The Taiwan Barbet playback served as a negative control to test whether passerine responses were specific to predator cues rather than a generalized reaction to conspicuous bird vocalizations. Responses to the control playback were not interpreted as mobbing but were used solely to verify predator specificity.

Each playback session lasted nine minutes, consisting of a 6-minute silence period followed by a 3-minute Collared Owlet playback. The 6-minute duration was adopted following the Taiwan Breeding Bird Survey protocol, which uses standardized stationary observation periods commonly applied in forested habitats in Taiwan (Lin et al. 2023). The initial silent period served as a baseline and acclimation phase, allowing birds to adjust to the presence of the observer and loudspeaker and enabling documentation of baseline presence, positions, and distances of potential responders prior to playback. Playbacks were broadcast using a loudspeaker (HANLIN-M53 Taiwan) placed approximately 10 m from the observer and positioned at ground level or low shrub height (≤ 1 m). The loudspeaker output was standardized to 80 ± 2 dB SPL at 1 m, verified with a handheld sound level meter (TES-1350A). All the trials were conducted with the same amplitude level.

During the first six minutes, all the passerine 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. This information was used solely to characterize baseline conditions and to identify individuals already close to the loudspeaker prior to playback. Because the silent and playback periods differed in duration, the silent period was not treated as a comparison treatment and no pre–post statistical analyses were conducted. During the following three-minute playback experiment, we quantified the presence of two distinct mobbing behaviors: 1) making alarm calls, defined as alarm or a violent acoustic vocalizations directed toward the playback source, and 2) approach, defined as individuals moving within a 10m radius of the loudspeaker. Because the experimental design relied solely on acoustic predator cues without a visible predator model, responses are interpreted as mobbing-like reactions to predator vocalizations rather than visual mobbing. The 10 m threshold was used as an operational definition of close, high-risk approach commonly adopted in playback studies (*e.g.*, Dutour et al. 2016), while response occurring beyond this distance are captured by the alarm-calling metric.

The individuals that were observed within 10m radius around the loudspeaker during the silent period were excluded from analyses as we could not confirm that whether the approaching behavior was the response to the playback or not. Only behavioral responses occurring during the playback period were included in subsequent analyses. The occurrence of either behavior was coded as a mobbing event (1), while the absence was coded as 0. 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. If we detected a living Collared Owlet or other predators within 50 m during the experiments, the test was canceled due to unknown effects with multiple mobbing targets. 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.

Supplementary control playback experiments

To determine whether passerines specifically reacted to predator cues rather than any bird vocalization, we conducted additional control trials using the call of the Taiwan Barbet, a non-predatory frugivore common in the same habitats. Control experiments were carried out at 15 out of the 48 intermediate elevation sites in Chiayi County in June 2022 and repeated at the same sites in February 2023. Each control trial began with six minutes of silence, followed by a three-minute Barbet playback and then a three-minute Owlet playback. The non-predatory control stimulus was presented first to avoid predator-induced suppression of subsequent responses. This sequence allowed direct comparison between control and predator stimuli while minimizing carryover effects. In the second stage, mobbing responses were recorded separately for the two playback types, while in the first stage, only the Owlet playback was used, providing an independent baseline dataset for cross-year comparison.

Data processing and statistical analyses

For the first stage of surveys, we focused on passerine responses to Collared Owlet calls. To test our hypothesis, we evaluated whether the probability of making alarm calls and approaching were influenced by season and elevation using generalized linear mixed models (GLMMs) with a binomial error structure and logit link, implemented in the lme4 package. Models for alarm calling and approaching were run separately. The fixed effects were season (breeding vs. non-breeding), elevation (low vs. intermediate), and the interaction between season and elevation. The random effects were species and site, accounting for repeated measurements and site-level variation. Statistical inference for seasonal effects refers to model-based main effects unless otherwise stated. All analyses were conducted using the software R (R Core Team 2018).

RESULTS

We conducted 148 rounds of playback experiments (breeding/intermediate: 43; breeding/low: 38; non-breeding/intermediate: 32; non-breeding/low: 36) during the first stage and observed 747 individuals. On average, 5.04 ± 3.23 individuals were observed and 2.38 ± 1.48 mobbed in each round. We recorded 476 individuals in breeding season, of which 147 individuals made alarm call (proportion of making alarm calls = 30.88%) and 122 individuals approached the loudspeaker within a 10m radius (proportion of approaching = 25.63%). Thirty-one species were observed during the breeding season and 22 species mobbed at least once (Table S1).

In non-breeding season, we recorded 271 individuals, of which 79 individuals made alarm call (proportion of making alarm calls = 29.15%) and 36 individuals approached the loudspeaker within a 10m radius (proportion of approaching = 13.28%). In non-breeding season, 32 species were observed and 22 species mobbed at least once. Morrison's Fulvetta (*Alcippe morrisonia*) was the species participating in mobbing activity the most in our experiments regardless of elevation level and season. In addition to Morrison's Fulvetta, White-bellied Erpornis (*Erpornis zantholeuca*) and Black-naped Monarch (*Hypothymis azurea*) also involved in mobbing activity in low elevation area, while Taiwan Yuhina (*Yuhina brunneiceps)* and Rufous-faced Warbler (*Abroscopus albogularis*) were most active in intermediate elevation area (Table S1).

Small passerine birds had similar likelihoods of making alarm calls in both breeding season and non-breeding season, as season was not a significant factor in influencing the probability of making alarm calls (Fig. 2; Table S2). However, they were less likely to approach the loudspeaker in the non-breeding season. The probability of approaching was significantly lower in non-breeding season than in breeding season (based on the main effect of season pooled across elevations) (Fig. 2; Table S3). The interaction between season and elevation was not significant, indicating that the seasonal effect on approaching behavior was consistent across elevation categories. Furthermore, the pattern of mobbing did not vary between elevation ranges at the community level.

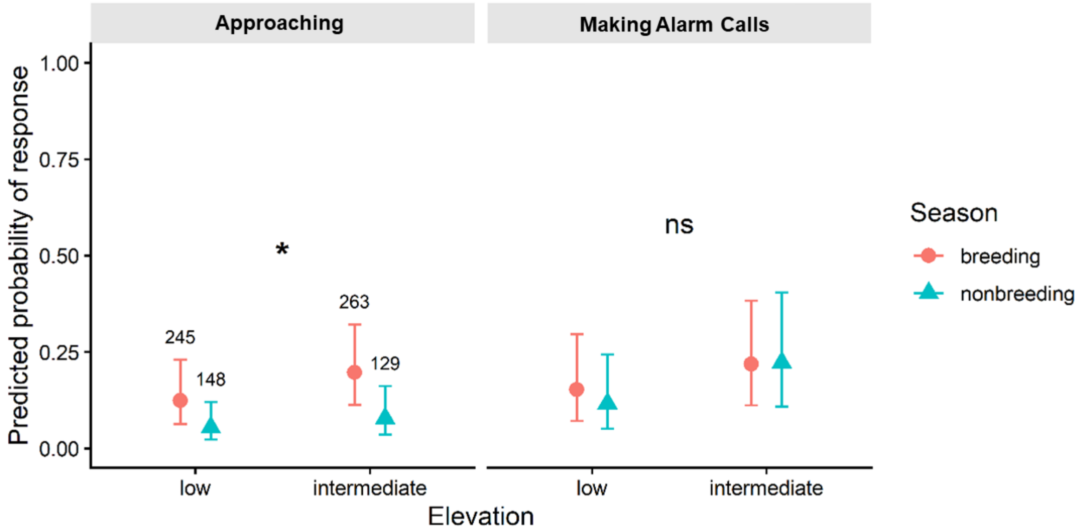

Fig. 2. Predicted probability (± 95% CI) of passerine approaching (left) and making alarm calls (right) responses to Collared Owlet playback across breeding and non-breeding seasons at low- and intermediate-elevation forest sites in Taiwan. Predictions were generated from binomial generalized linear mixed models including season and elevation as fixed effects and species and site as random effects. Numbers above error bars (left panel) indicate sample sizes for each season–elevation combination; the same samples were used for mobbing analyses (right panel). The asterisk indicates a significant main effect of season on approaching behavior pooled across elevations ($p < 0.01$), whereas "ns" denotes a non-significant main effect of season for making alarm calls.

We conducted additional control trials during stage 2 (June 2022 and February 2023) in which the non-predatory Taiwan Barbet was played immediately before the standard Collared Owlet playback. During the breeding season, only a small fraction of individuals responded to the Barbet control (6 of 114 individuals), whereas a much larger fraction mobbed in response to the subsequent

Owlet playback at the same sites (63 of 120 individuals). A similar pattern was observed in the non-breeding season, with consistently low mobbing proportions to Barbet and higher mobbing proportions to Owlet (Fig. 3). Chi-square tests confirmed that mobbing proportions differed significantly between Barbet and Owlet stimuli in both seasons, indicating that the observed responses represent predator-specific anti-predator behavior rather than generalized reactions to any loud bird call.

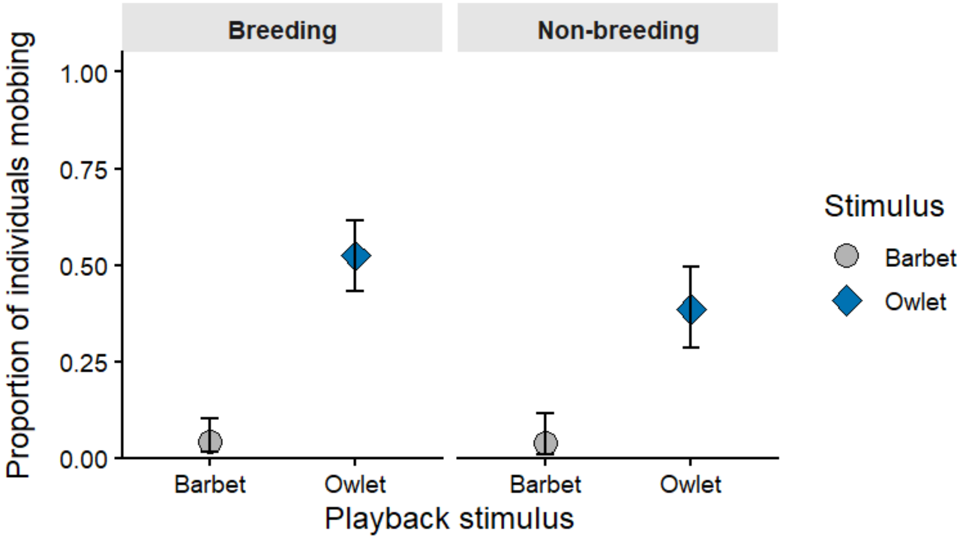

Fig. 3. Comparison of passerine mobbing responses to non-predatory (Taiwan Barbet; gray circles) and predatory (Collared Owlet; blue diamonds) playback stimuli during stage 2 experiments. Each point represents the proportion of individual birds that exhibited mobbing behavior out of all individuals detected during that playback segment, and vertical error bars indicate binomial 95% confidence intervals.

DISCUSSION

Our playback experiment demonstrated clear seasonal differences in the mobbing strategies within the passerine community in Taiwan. While small passerine birds produced alarm calls at comparable frequencies in both seasons, they were markedly less likely to approach the predator cue during the non-breeding season. This pattern supports our hypothesis that the small passerine birds perform riskier or more escalated forms of anti-predator behavior during the breeding season, when reproductive investment is high, than during the non-breeding season.

The stronger mobbing response observed in the breeding season aligns with most previous heightened anti-predator behavior when reproductive investment is high (Root 1969; Shedd 1982; 1983; Shimazaki et al. 2017; Zimmermann and Curio 1988, but see Cunha et al. 2017 and Dutour et al. 2019). Seasonal variation of mobbing has often been linked to breeding activities, during which adults defend nests, mates, and territories. Although close approach to a predator carries substantial mortality risk to breeding adults, the fitness costs associated with nest failure or loss of dependent offspring may outweigh these risks, favoring escalation of anti-predator behavior during the breeding season. Elevated testosterone levels in breeding season regulate behavior such as display (da Cunha et al. 2017), incubation (Balthazart 1983; De Jong et al. 2016), mate competition, and defending territory (Wingfield et al. 1987), and may simultaneously enhance willingness to engage in risky anti-predator actions. Mobbing may also play a role in social learning, as juveniles observing adults can acquire predator-recognition skills that benefit them in the subsequent season (Griesser and Suzuki 2017). A contrasting pattern occurs in species with year-round territoriality, where reproductive constraints may be similar across seasons, resulting little seasonal difference in mobbing response (da Cunha et al. 2017). Together, these findings suggest that breeding status, and the reduced opportunity to flee when reproductive resources must be defended, is one of the important drivers of seasonal changes in anti-predator behaviors. Similarly, Scott and Robinson (2023) showed that songbirds responding to pygmy-owl vocalizations modulated close approach behavior according to perceived risk, consistent with our finding that approach represents a higher-risk component of mobbing that varies seasonally.

Predator diet composition can also shape the mobbing behavior, as prey species tend to react more strongly to predators that pose a higher predation risk. Dutour et al. (2017) demonstrated that predators with a greater prevalence of birds in their diet elicit more intense mobbing, and species that frequently preyed upon respond more aggressively. Seasonal diet changes in owl species are well documented (Korpimäki 1986), and several *Glaucidium* species shift toward a more passerine-prevalence diet during winter (Mikkola 1983; Solheim 1984). For example, studies on Eurasian

Pygmy Owls (*G. passerinum*) indicate increased reliance on small birds outside the breeding season, coinciding with reduced insect availability (Mikkola 1983; Solheim 1984). Although detailed dietary information for Collared Owlets in Taiwan remains limited, existing studies indicate an insect-dominated diet in the breeding season (Tseng and Lin 2012), suggesting lower predation pressure on passerines during this period. Local observations suggest increased consumption of small passerines in the non-breeding season (W.L. Lin, personal communication). Together, evidence from congeners supports the inference that Collared Owlets likely pose a higher avian predation risk during winter. Such a seasonal increase in predation risk may promote a more cautious strategy, in which passerines maintain alarm calling while avoiding close approach, helping to explain why approaching behavior declined markedly in winter, whereas making alarm calls remained comparable across season. Although winter flocking could be expected to facilitate group escalation, our results instead suggest that flocking individuals primarily maintain safer distances, consistent with collective risk assessment rather than close-range mobbing. Our results are consistent with the idea that passerines adjust the intensity of their mobbing according to the perceived threat posed by the predator.

We did not detect differences in the probability of making alarm calls and approaching between the two elevation ranges, suggesting that variation in community composition between elevations (Table S1) did not translate into differences in mobbing behaviors. A likely explanation is that Morrison’s Fulvetta, the dominant mobber to the Collared Owlet in our study, occurs widely across elevations and responded strongly to the Collared Owlet call at both sites. As a small subcanopy species that is vulnerable to *Glaucidium* predation (da Cunha et al. 2017; Lima et al. 2018), its consistent behavior may have masked variation contributed by less common species. Seasonal altitudinal movements may also have reduced community differences. For instance, Taiwan Yuhina shifted from intermediate downward to lower elevations during the non-breeding season, increasing bird community similarity between sites. Such seasonal mixing of species could dilute elevational contrasts in mobbing responses.

Most studies quantify mobbing primarily by whether individuals approach their predators or its cue (Dutour et al. 2016; Dutour et al. 2017; Sandoval and Wilson 2012; Tilgar and Moks 2015). Yet, alarm call also plays a critical role in anti-predator strategy, particularly as a lower-risk means of alerting conspecifics and deterring predators (Kareksela et al. 2013). Identifying callers can be problematic in species-rich soundscapes (Haselmayer and Quinn 2000; Sandoval and Wilson 2012), leading some studies to exclude vocal responses. In our playback trials, however, only a small number of individuals were typically present (5.03 ± 3.23 individuals recorded per site), allowing us to reliably determine whether alarm calls occurred. The contrasting seasonal patterns in our results, stable calling rates but reduced approaching in winter, highlight the value of treating these behaviors as complementary components of mobbing. We therefore encourage future research to consider both alarm calls as well as approaching behavior to better characterize variation in anti-predator strategies.

To verify that seasonal differences were not artifacts of any loud acoustic playback, we conducted a second stage of playback experiments using the Taiwan Barbet, a non-predatory frugivore, as a control stimulus. Passerines showed markedly weaker responses to Barbet calls than to Collared Owlet calls in both breeding and non-breeding seasons, demonstrating that individuals discriminated between predator and non-predator cues. This predator specificity held even when analyses were restricted to intermediate-elevation sites shared by both stages. The contrast between treatments provides strong evidence that the seasonal decline in approaching behavior reflects reduced willingness to initiate mobbing under higher predation risk, rather than a generalized decline in responsiveness.

The control playback experiments were conducted several years after the initial Collared Owlet playback surveys. Although this temporal gap could potentially influence community composition, the control stage was designed to test predator specificity rather than to provide a direct temporal or seasonal comparison with the owl playback experiments. Forest structure and habitat characteristics at the study sites remained largely unchanged over this period, and the passerine community composition relevant to community-level responses was stable. Therefore, the temporal separation between experimental stages is unlikely to affect our main inference regarding predator-specific responses.

Breeding status is widely considered a main driver of seasonal variation in mobbing behavior, and our findings are consistent with this view. At the same time, seasonal shifts in predator diet, well documented for several *Glaucidium* owls, likely contribute to changes in perceived predation risk and therefore to variation in mobbing intensity. Our results suggest that both mechanisms may operate together: passerines exhibit escalated mobbing during the breeding season, when reproductive investment constrains their ability to flee, and adopt safer strategies in winter, when owlets appear to rely more heavily on small birds as prey. Future studies incorporating detailed dietary analyses and experimental manipulations of perceived risk will help elucidate how these factors shape the anti-predator strategies.

CONCLUSIONS

Our study demonstrates that passerine communities mob a diurnal owl in both breeding and non-breeding seasons, but adjust the intensity of higher-risk behaviors across seasons. While alarm calling remained consistent, approaching occurred more frequently in the breeding season, suggesting that passerines reduce risky behaviors when predation pressure is higher in the non-breeding season. Elevation did not influence community-level responses, likely due to shared dominant mobbing species across sites. Supplementary control playbacks further confirmed that mobbing responses were specific to predator cues. Together, these findings highlight flexible, context-dependent anti-predator strategies in passerine communities.

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Authors' contributions: DCC: Methodology, investigation, formal analysis, writing - original draft. JST: Conceptualization, investigation, writing - review and editing, resources, supervision.

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Ethics approval consent to participate: Not applicable. No birds were captured during the study. The experiments comply with the current laws of Taiwan.

RERERENCES

Bachman GC. 1993. The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. Anim Behav **46:**233–244. doi:10.1006/anbe.1993.1185.

Balthazart J. 1983. Hormonal correlates of behavior. Avian Biol. No. 7. p 221–365. Elsevier.

Bērziņš A, Krama T, Krams I, Freeberg TM, Kivleniece I, Kullberg C et al. 2010. Mobbing as a trade-off between safety and reproduction in a songbird. Behav Ecol **21:**1054–1060. doi:10.1093/beheco/arq104.

Betts MG, Hadley AS, Doran PJ. 2005. Avian mobbing response is restricted by territory boundaries:experimental evidence from two species of forest warblers. Ethology **111:**821–835. doi:10.1111/j.1439-0310.2005.01109.x.

Bose M, Guidali F. 2001. Seasonal and geographic differences in the diet of the barn owl in an agro-ecosystem in northern Italy. J Raptor Res **35:**240–246.

Brown G, Shine R. 2004. Effects of reproduction on the antipredator tactics of snakes

(*Tropidonophis mairii*, Colubridae). Behav Ecol Sociobiol **56:**257–262. doi:10.1007/s00265-004-0778-5.

Caro T. 2005. Antipredator defenses in birds and mammals. University of Chicago Press.

Carrera JD, Fernández FJ, Kacoliris FP, Pagano L, Berkunsky I. 2008. Field notes on the breeding biology and diet of Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) in the dry Chaco of Argentina. Ornitología Neotropical **19:**315–319.

Collias NE, Collias EC. 2014. Nest building and bird behavior. Princeton University Press.

Curio E, Ernst U, Vieth W. 1978a. The adaptive significance of avian mobbing. Ethology **48:**184–202. doi:10.1111/j.1439-0310.1978.tb00254.x.

Curio E, Ernst U, Vieth W. 1978b. Cultural transmission of enemy recognition:one function of mobbing. Science **202:**899–901.

da Cunha FCR, Fontenelle JCR, Griesser M. 2017. Predation risk drives the expression of mobbing across bird species. Behav Ecol **28:**1517–1523. doi:10.1093/beheco/arx111.

De Jong B, Lens L, Amininasab SM, van Oers K, Darras VM, Eens M et al. 2016. Effects of experimentally sustained elevated testosterone on incubation behaviour and reproductive success in female great tits (*Parus major*). Gen Comp Endocrinol **230:**38–47. doi:10.1016/j.ygcen.2016.02.017.

Denson RD. 1979. Owl predation on a mobbing crow. The Wilson Bulletin **91:**133–133.

Dutour M, Cordonnier M, Léna J-P, Lengagne T. 2019. Seasonal variation in mobbing behaviour of passerine birds. J Ornithol**:**1–6. doi:10.1007/s10336-019-01630-5

Dutour M, Léna J-P, Lengagne T. 2016. Mobbing behaviour varies according to predator dangerousness and occurrence. Anim Behav **119:**119–124. doi:10.1016/j.anbehav.2016.06.024.

Dutour M, Léna JP, Lengagne T. 2017. Mobbing behaviour in a passerine community increases with prevalence in predator diet. Ibis **159:**324–330. doi:10.1111/ibi.12461.

Fang W-H, Hsu Y-H, Lin W-L, Yen S-C. 2020. The function of avian mobbing:an experimental test of 'attract the mightier' hypothesis. Anim Behav **170:**229–233.

doi:10.1016/j.anbehav.2020.10.013.

Flasskamp A. 1994. The adaptive significance of avian mobbing V. An experimental test of the 'move on'hypothesis. Ethology **96:**322–333. doi:10.1111/j.1439-0310.1994.tb01020.x.

Gaynor KM, Brown JS, Middleton AD, Power ME, Brashares JS. 2019. Landscapes of fear:spatial patterns of risk perception and response. Trends Ecol Evol **34:**355–368. doi:10.1016/j.tree.2019.01.004.

Gehlbach FR, Leverett JS. 1995. Mobbing of Eastern Screech-owls:predatory cues, risk to mobbers and degree of threat. Condor **97:**831–834. doi:10.2307/1369196.

Gillies CS, Beyer HL, St Clair CC. 2011. Fine-scale movement decisions of tropical forest birds in a fragmented landscape. Ecol Appl **21:**944–954. doi:10.1890/09-2090.1.

Griesser M, Suzuki TN. 2017. Naïve juveniles are more likely to become breeders after witnessing predator mobbing. Am Nat **189:**58–66.

Haselmayer J, Quinn JS. 2000. A comparison of point counts and sound recording as bird survey methods in Amazonian southeast Peru. Condor **102:**887–893. doi:10.1093/condor/102.4.887.

Hill DA. 1997. Seasonal variation in the feeding behavior and diet of Japanese macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. Am J Primatol **43:**305–320. doi:10.1002/(SICI)1098-2345(1997)43:4<305::AID-AJP2>3.0.CO;2-0.

Houston AI, McNamara JM, Hutchinson JM. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philos Trans R Soc Lond **341:**375–397. doi:10.1098/rstb.1993.0123.

Inger R, Bearhop S, Robinson JA, Ruxton G. 2006. Prey choice affects the trade-off balance between predation and starvation in an avian herbivore. Anim Behav **71:**1335–1341. doi:10.1016/j.anbehav.2005.08.015.

Jiménez JE, Jaksić FM. 1989. Biology of the Austral pygmy-owl. Wilson Bull**:**377–389.

Kareksela S, Härmä O, Lindstedt C, Siitari H, Suhonen J. 2013. Effect of Willow Tit Poecile montanus alarm calls on attack rates by Pygmy Owls *Glaucidium passerinum*. Ibis **155:**407–

412. doi:10.1111/ibi.12026.

Korpimäki E. 1986. Seasonal changes in the food of the Tengmalm's owl *Aegolius funereus* in western Finland. In:Ann Zool Fenn. p 339–344.

Krama T, Krams I. 2004. Cost of mobbing call to breeding pied flycatcher, *Ficedula hypoleuca*. Behav Ecol **16:**37–40. doi:10.1093/beheco/arh116.

Krams I, Bērziņš A, Krama T. 2009. Group effect in nest defence behaviour of breeding pied flycatchers, *Ficedula hypoleuca*. Anim Behav **77:**513–517. doi:10.1016/j.anbehav.2008.11.007.

Krams I, Krama T. 2002. Interspecific reciprocity explains mobbing behaviour of the breeding chaffinches, *Fringilla coelebs*. Proceedings of the Royal Society of London. Series B:Biological Sciences **269:**2345–2350. doi:10.1098/rspb.2002.2155.

Krams I, Krama T, Igaune K, Mänd R. 2008. Experimental evidence of reciprocal altruism in the pied flycatcher. Behav Ecol Sociobiol **62:**599–605. doi:10.1007/s00265-007-0484-1.

Lee C-L, Huang Y-R, Shen C-W, Liu W-S. 2006. Study on the Recovery of Understory Vegetation of Cryptomeria japonica Plantations in Sitou, Central Taiwan. J Exp For NTU **20:**299–307.

Lima HSd, Las-Casas FMG, Ribeiro JR, Gonçalves-Souza T, Naka LN. 2018. Ecological and phylogenetic predictors of mobbing behavior in a tropical dry forest. Ecology and evolution **8:**12615–12628.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation:a review and prospectus. Can J Zool **68:**619–640. doi:10.1139/z90-092.

Lin D-L, Ko JC-J, Amano T, Hsu C-T, Fuller RA, Maron M et al. 2023. Taiwan's Breeding Bird Survey reveals very few declining species. Ecol Indicators **146:**109839. doi:10.1016/j.ecolind.2022.109839.

Mikkola H. 1983. Owls of europe. T. & AD Poyser.

Motta-Junior JC. 2007. Ferruginous Pygmy-owl (*Glaucidium brasilianum*) predation on a mobbing Fork-tailed Flycatcher (*Tyrannus savana*) in south-east Brazil. Biota Neotrop **7:**0–0. doi:10.1590/S1676-06032007000200038.

Pavey CR, Smyth AK. 1998. Effects of avian mobbing on roost use and diet of powerful owls, *Ninox strenua*. Anim Behav **55:**313–318. doi:10.1006/anbe.1997.0633.

Pettifor RA. 1990. The effects of avian mobbing on a potential predator, the European kestrel, *Falco tinnunculus*. Anim Behav **39:**821–827. doi:10.1016/S0003-3472(05)80945-5.

R Core Team. 2018. R:A language and environment for statistical computing.

Root RB. 1969. The behavior and reproductive success of the blue-gray gnatcatcher. Condor **71:**16–31. doi:10.2307/1366044.

Sandoval L, Wilson DR. 2012. Local predation pressure predicts the strength of mobbing responses in tropical birds. Curr Zool **58:**781–790. doi:10.1093/czoolo/58.5.781.

Scott M, Robinson WD. 2023. Mobbing behavior of songbirds in response to calls of an ambush-predator, the Northern Pygmy-Owl. Front Ecol Evol **11:**1092323. doi:10.3389/fevo.2023.1092323.

Shedd DH. 1982. Seasonal variation and function of mobbing and related antipredator behaviors of the American robin (*Turdus migratorius*). The Auk, pp. 342–346.

Shedd DH. 1983. Seasonal variation in mobbing intensity in the Black-capped Chickadee. Wilson Bull, pp. 343–348.

Shimazaki A, Yamaura Y, Senzaki M, Yabuhara Y, Nakamura F. 2017. Mobbing call experiment suggests the enhancement of forest bird movement by tree cover in urban landscapes across seasons. Avian Conserv Ecol **12:**Article 16. doi:10.5751/ACE-01013-120116.

Silva-Porto F, Cerqueira R. 1990. Seasonal variation in the diet of the Burrowing Owl *Athene cunicularia* in a restinga of Rio de Janeiro state. Cienc Cult **42:**1182–1186.

Solheim R. 1984. Caching behaviour, prey choice and surplus killing by Pygmy Owls *Glaucidium passerinum* during winter, a functional response of a generalist predator. *In*: Ann Zool Fenn, pp. 301–308.

Templeton CN, Greene E, Davis K. 2005. Allometry of alarm calls:black-capped chickadees encode information about predator size. Science **308:**1934–1937. doi:10.1126/science.110884.

Tilgar V, Moks K. 2015. Increased risk of predation increases mobbing intensity in tropical birds of

French Guiana. J Trop Ecol **31:**243–250. doi:10.1017/S0266467415000061.

Tome D. 1994. Diet composition of the long-eared owl in central Slovenia:seasonal variation in prey use. J Raptor Res **28:**253–258. doi:10.1016/S0003-3472(88)80175-1.

Tseng Y-S, Lin W-L. 2012. Breeding biology of Collared Owlet (*Glaucidium brodiei pardalotum*). Note News Wildl **16:**34–40.

Wingfield JC, Ball GF, Dufty AM, Hegner RE, Ramenofsky M. 1987. Testosterone and aggression in birds. Am Sci **75:**602–608.

Zimmermann U, Curio E. 1988. Two conflicting needs affecting predator mobbing by great tits, *Parus major*. Anim Behav **36:**926–932.

Supplementary materials

Table S1. Species recorded during Phase 1 playback experiments and the number of individuals exhibiting mobbing behavior (mobbing/total observed) across breeding and non-breeding seasons at low and intermediate elevations. Mobbing behavior includes alarm calling or approaching the playback source. (download)

Table S2. Parameter estimates and 95% confidence intervals from the binomial GLMM testing effects of season, elevation, and their interaction on the probability of mobbing toward Collared Owlet playback during Phase 1 surveys. Season reference level = breeding; elevation reference level = low. Species and site were included as random intercepts. (download)

Table S3. Parameter estimates and 95% confidence intervals from the binomial GLMM testing effects of season, elevation, and their interaction on the probability of approaching behavior toward Collared Owlet playback during Phase 1 surveys. Season reference level = breeding; elevation reference level = low. Species and site were included as random intercepts. (download)