

Human disturbance provides foraging opportunities for birds in primary subalpine forest

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Abstract Interspecific foraging associations are well-documented phenomena, characterized by one or more species exploiting the behavior of another species to decrease predation or increase foraging success. In rare cases, birds directly exploit human behavior, but examples of these interactions are limited to species that naturally occur in edge, open, or disturbed habitats. With observations and experiments we provide evidence of insectivorous birds exploiting human disturbance in primary subalpine forest in the mountains of southern China, displaying behavioral flexibility to gain novel foraging opportunities. We cut and cleared small swaths of dense bamboo growth for an unrelated study. Multiple insectivorous species were recruited to the cleared areas, foraging extensively in the disturbed earth, often within 1 m of us. These species included *Tarsiger chrysaeus*, *Tarsiger indicus*, *Cettia*

brunnifrons or *Cettia major*, and *Heteroxenicus stellatus*. This behavior is likely a modification of pre-existing interspecific foraging associations with pheasants and large mammals in the region. These larger animals disturb the earth and lower vegetation layers upon passage and while foraging, exposing previously inaccessible invertebrate prey items on which small insectivorous birds can feed. Our findings highlight a behavioral capacity in birds to utilize human disturbance in an ecosystem with limited human presence.

Keywords Adaptive foraging · Interspecific foraging associations · Human disturbance · Hengduan Mountains · Gongga Mountain · Seasonality

Zusammenfassung

Menschlicher Einfluss liefert Vögeln im subalpinen Primärwald eine Gelegenheit zur Nahrungssuche

Beziehungen zwischen Arten bei der Nahrungssuche sind gut dokumentierte Phänomene, welche dadurch gekennzeichnet sind, dass eine oder mehrere Arten das Verhalten einer anderen Art nutzen, um ihr Prädationsrisiko zu verringern oder den Erfolg bei der Nahrungssuche zu erhöhen. In seltenen Fällen nutzen Vögel menschliches Verhalten direkt, allerdings sind Beispiele solcher Interaktionen auf Arten beschränkt, die natürlicherweise in Randhabitaten oder in offenen oder Ruderallebensräumen vorkommen. Durch Beobachtungen und Experimente liefern wir Belege dafür, wie insektenfressende Vögel menschliche Einflussnahme im subalpinen Primärwald in den Bergen Südchinas nutzen und dabei eine Verhaltensflexibilität zeigen, welche es ihnen ermöglicht, neue Futterquellen aufzutun. Für eine

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unabhängige Untersuchung mähten wir schmale Streifen dichter Bambusbestände und entfernten das Mähgut. Eine Vielzahl insektenfressender Arten wurde von den gerodeten Flächen angezogen und suchte im aufgebrochenen Erdboden nach Nahrung, oft weniger als einen Meter von uns entfernt. Zu diesen Arten gehörten: *Tarsiger chrysaeus*, *T. indicus*, *Cettia brunnifrons* oder *C. major* sowie *Heteroxenicus stellatus*. Diese Verhaltensweise stellt wahrscheinlich eine Modifikation bereits existierender interspezifischer Beziehungen bei der Nahrungssuche zu Fasanen und Großsäugern in der Region dar. Diese größeren Tiere bringen beim Vorbeilaufen und auf der Futtersuche den Erdboden und die unteren Vegetationsschichten durcheinander und fördern dabei zuvor unzugängliche wirbellose Beutetiere zutage, von welchen sich kleine insektivore Vögel ernähren können. Unsere Befunde zeigen bei Vögeln ein Verhaltenspotenzial zur Nutzung menschlicher Einflussnahme in einem Ökosystem mit eingeschränkter menschlicher Präsenz auf.

Introduction

Almost 70 years ago, Lack (1948) noted an exceptional foraging behavior in the European Robin (*Erithacus rubecula*): robins will follow Common Pheasants (*Phasianus colchicus*), keeping close and feeding on invertebrates in the earth disturbed by the pheasants. Buffon (1771–1783) noted a similar behavior centuries before, observing that European Robins were attracted to humans, often following travelers through the forest. The robins described by Lack (1948) and Buffon (1771–1783) were tame and unafraid of game birds and large mammals, including humans. It has been suggested that these birds are, in fact, attracted to larger-bodied birds and mammals that break up the ground and disturb the leaf litter upon passage (Lack 1948), exposing invertebrate prey items hidden beneath the surface. Given their size and anatomy, robins are unable to turn over large debris and leaf litter (Lack 1948), thus this foraging strategy provides access to previously inaccessible prey. The foraging behaviors observed by Lack (1948) and Buffon (1771–1783) have fascinated observers since their description, but explicit tests to better understand these behaviors are rarely performed. In this study we coupled behavioral observations of insectivorous birds exploiting human disturbance with experimental manipulation to extend our understanding of this adaptive foraging strategy first described by Buffon (1771–1783) in the 18th century.

Interspecific foraging associations have been documented in a diversity of avian taxa. For example, birds often follow and forage in association with Army Ant

swarms and non-human primates, or other large mammals (Rand 1953; Dean and MacDonald 1981; Zhang and Wang 2000; Kuniy et al. 2003; Beiseigel 2007; King and Cowlishaw 2008; Willis and Oniki 1978). The follower benefits from increased foraging opportunities as the other animals flush and expose prey items. Given the repeated evolution of interspecific foraging associations (see Heymann and Hsia 2015), and the limited geographic scope of foraging association studies (confined mostly to the Neotropics) (King and Cowlishaw 2008), these interactions are likely more taxonomically and geographically widespread than currently recognized.

Evidence of human/bird foraging associations are largely limited to species that naturally occur in edge, open, and/or disturbed habitats, such as animals that utilize urban and agricultural environments (Rand 1953; Dugatkin 2013). It is no surprise, or coincidence, that birds that have evolved to occupy disturbed and open habitats have flourished in human-modified environments through association with human activities, such as New World blackbirds (family Icteridae) foraging behind tractors (Beasley and Carothers 1974) and European Robins (*Erithacus rubecula*) foraging in association with gardeners and gravediggers (Lack 1948). Less common, however, is evidence that birds can exploit human activities in old-growth forest.

Here, we present evidence that insectivorous birds can exploit human disturbance in primary subalpine forest in the mountains of southern China. In our research we routinely cut and clear small swaths of dense bamboo in the forest to erect mist nets to catch birds. We observed insectivorous species that were attracted to the recently cleared mist-net lanes, foraging in the disturbed earth and bamboo cuttings, often within a few meters of us. Following our initial observations, we experimentally tested the hypothesis that insectivorous birds are attracted to, and utilize, habitat disturbance.

Methods

Study site

We conducted this study in Gongga Shan National Nature Reserve, Sichuan, China (latitude 29°34' 21.6084" N, longitude 101°59' 10.6188"E). Mount Gongga, which is located within the reserve, is the easternmost peak in Asia above 7000-m elevation and is located in the central Hengduan Mountains of southern China. The Hengduan Mountains form the southeastern edge of the Tibetan Plateau and western margin of the Sichuan Basin, spanning steep elevational and environmental gradients. In these mountains, bird habitats extend from subtropical lowlands

to alpine meadows. We conducted our study at subalpine elevations on the eastern slope of Mount Gongga, where the forest is dominated by a tall conifer (*Abies fabri*) canopy, rhododendron (*Rhododendron vernicosum*) mid-story, and dense bamboo (*Sinarundinaria* spp.) understory.

The mountains of southern China harbor unparalleled temperate diversity (Fjeldså et al. 2012). To date, 939 bird species are recognized from this region (Wu et al. 2016). These mountains are the center of diversity for pheasants (family Phasianidae) (del Hoyo et al. 2005), and seven species of pheasant occur in Gongga Shan National Nature Reserve (Zhou et al. 2014). These large birds disturb the ground layer as they forage. In addition, large mammals that also disturb the ground layer are diverse in the mountains of southern China. These mammals include badgers (family Mustela), Asiatic bears and pandas (family Ursidae), and numerous species of ungulates, like Takin and other bovids (*Budorcas taxicolor*; family Bovidae), Wild Boar (*Sus scrofa*), and deer (family Cervidae).

The Hengduan Mountains experience dramatic seasonal fluctuations in climate because of their temperate latitude. At middle and upper elevations, snow covers the ground for much of the winter and daily winter temperatures routinely drop below freezing (Fig. 1). At 3000-m elevation, minimum daily temperatures can vary

by as much as 25 °C between winter and summer (Fig. 1). In response to this seasonality, the majority of montane birds seasonally migrate across elevations to escape harsh winter conditions at upper elevations (del Hoyo et al. 2005). These altitudinal migrants return to breeding elevations in spring as snows thaw and temperatures warm. In Gongga Shan National Nature Reserve, we have recorded altitudinal migrants arriving to breeding elevations above 3000 m as early as March, but the majority of spring migration to these upper elevations occurs in April and early May (unpublished data of the authors). By June, most species that breed above 3000 m have already started breeding. During the transition from winter to summer (March–June), migrants can experience unexpected snowstorms and high degrees of climatic variability (Fig. 1).

Initial observations and controlled experiments

On 4 and 5 May 2015, while mist-netting birds for an unrelated study at 3250-m elevation on the eastern slope of Mount Gongga, we observed that insectivorous birds were attracted to our disturbance, foraging in the disturbed earth along cleared mist-net lanes. To erect mist nets, we cut and cleared dense bamboo to create lanes 1.5 m wide and 12 m long in primary subalpine forest.

On 9–12th June 2015, we returned to Gongga to collect video footage of birds foraging in disturbed net lanes (Fig. 2; Online Appendix) and experimentally test the hypothesis that birds are recruited to habitat disturbance. In the experiment we simulated standardized net-lane clearing because this disturbance is uniquely human and because we initially observed birds foraging in our net lanes, allowing

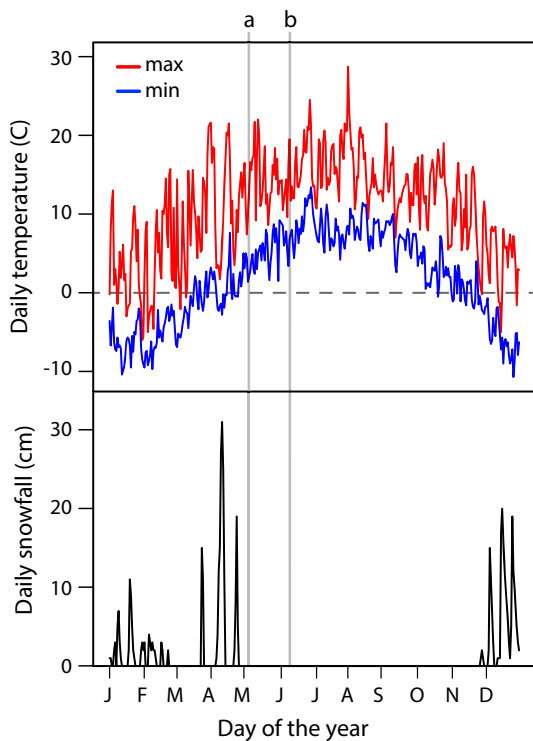


Fig. 1 Daily temperature and snowfall at 3000-m elevation on the eastern slope of Mount Gongga, 2015. X-axis marks indicate the first day of each month. a Indicates the date of the initial observations, b indicates the date of the controlled experiments



Fig. 2 Still photograph from a video (Online Appendix) showing a female-plumaged White-browed Bush-robin (*Tarsiger indicus*) foraging in a recently cleared net lane

us to make comparisons between our initial observations and the experiment. The experiment was as follows:

1. Two video cameras were placed facing each other in the bamboo understory, 10–12 m apart and 1 m off the ground.
2. S. G. D. and Y. W. were each positioned at the base of a camera, where they remained silent for 10 min before beginning the control treatment. This 10-min buffer period ensured that the birds observed were not recruited to the area by our noise and movements as we entered the area and set up cameras.
3. We then began the control treatment, observing and recording the presence of birds for 20 min in the undisturbed bamboo between the cameras. Birds were recorded as “present” if they crossed the transect between the cameras within 3 m of the ground. We made visual observations, which were corroborated with video footage to ensure that all birds present were recorded.
4. Following the control treatment, S. G. D. and Y. W. cut a 1.5-m-wide lane between the cameras for 10 min, cutting the bamboo at its base and trampling the vegetation and ground layer. This method disturbed the topsoil and leaf litter layer.
5. After the disturbance, we resumed our positions at the cameras, observing and recording the presence of birds in the disturbed area between the cameras for the next 20 min. Birds were recorded for the disturbance treatment following similar protocols as the control treatment.

We conducted eight paired replicates of the above experiment.

The nature of the disturbance treatment prevented us from conducting the disturbance treatments before the controls at the same site. However, we performed two additional replicates for each treatment at independent sites. That is, for two additional control replicates we performed steps 1–3 without subsequently performing steps 4 and 5, and for two additional disturbance replicates we performed steps 1, 4, and 5 to the exclusion of steps 2 and 3. If the ordering of the paired treatments increases bird recruitment in the disturbance treatment, negatively biasing the experiment, then we would expect fewer relative recruitment events for the disturbance treatment during independent replicates compared to paired replicates. All experimental replicates (totaling ten replicates for each treatment) were conducted between 3000- and 3300-m elevation, 50–100 m apart, and in areas with similar habitat structure. Based on the results outlined below, we are confident that a distance of >50 m among replicates was sufficient to avoid biases associated with pseudoreplication (i.e., detecting the same individual in multiple replicates).

Results

Initial observations

In May 2015, we observed four species (*Cettia brunifrons* or *Cettia major*, *Heteroxenicus stellate*, *Tarsiger chrysaesus*, *Tarsiger indicus*) foraging on the disturbed earth beneath cleared mist net lanes. On one occasion, two male-plumaged *T. chrysaesus* foraged within 5 m of each other for approximately 5 min, before one chased the other away. On another occasion, a female-plumaged *T. indicus* appeared and began foraging in the cleared areas as we were cutting bamboo. This bird continued to forage alongside us despite the chaos and noise of our clearing efforts, often coming within 1 m of us. After this net lane was cleared, we observed three distinct individuals (two female-plumaged *Tarsiger indicus* and one male-plumaged *Tarsiger chrysaesus*) foraging within the 12-m net lane. On multiple occasions we observed more than one individual foraging at a given time in the cleared net lane in an otherwise dense bamboo understory. At no point did any of the birds appear to be disturbed by our presence.

Controlled experiment

We observed increases in bird recruitment in the disturbance treatment (Fig. 3). We observed birds in six of the disturbance replicates (eight birds total) and in one of the control replicates (one bird total). The increase in birds observed in the disturbance treatment from the control treatment was statistically significant in a one-tailed Fisher’s exact test ($p = 0.029$), testing the alternative hypothesis that recruitment increases with disturbance. In contrast to our initial observations, at no point during the experiment did we observe more than one bird at a time foraging in the cleared lane, nor did we observe birds during the 10-min cutting period. Interestingly, only three of the eight birds recorded in the disturbance treatment were observed foraging in the lane. The remaining five individuals landed in the cleared area or flew across the transect without foraging during the 20-min observation period. The birds observed during the disturbance treatment were: one male *Tarsiger chrysaesus*, two female-plumaged *Tarsiger chrysaesus*, two female-plumaged *Tarsiger indicus*, one *Ficedula strophiate*, and two unidentified passerines. We did not observe birds in the independent control treatments, but we observed birds in both independent disturbance replicates, suggesting that the ordering of the paired treatments did not negatively bias the experiment.

We identified two possible instances of pseudoreplication: first, a female-plumaged *T. chrysaesus* was

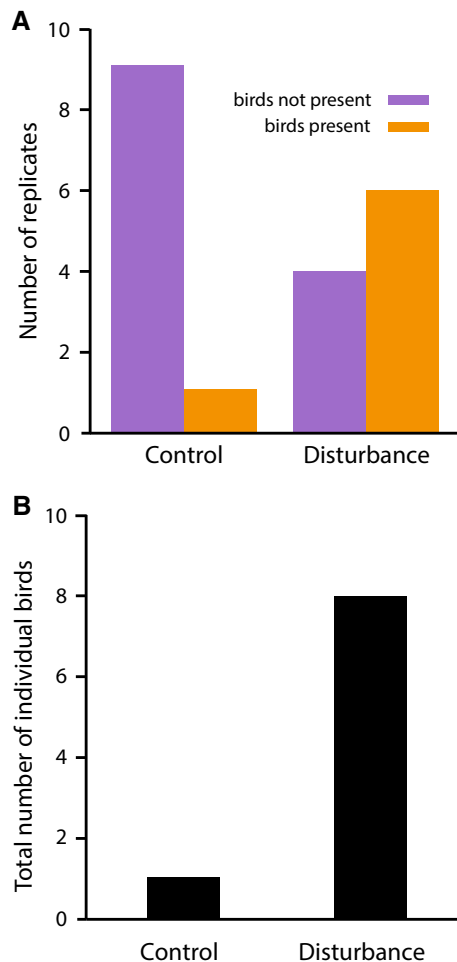


Fig. 3 Experimental results testing if birds are attracted to disturbance. **a** The number of experimental replicates in which birds were observed. **b** The total number of individual birds observed in each experimental treatment ($n = 10$ replicates/treatment)

recorded in two replicates that were 75 m apart. We cannot be positive that these birds were not the same individual, but our results would remain unchanged even if they were because both of these experiments had other birds present. If we remove this individual from the dataset (or attribute it to only one of the replicates) the result remains the same because the number of birds recruited in each replicate is not taken into account in the Fisher's exact test, only whether birds were present or absent in a replicate. Second, a female-plumaged *T. indicus* was recorded during two replicates that were 135 m apart. These experiments were done in an area that we previously surveyed for *T. indicus* the month before. We know that these two replicates were in distinct *T. indicus* territories with an additional territory situated between. These two lines of evidence suggest that pseudoreplication did not bias our results or interpretations.

Discussion

The experimental results, paired with the initial observations, support the hypothesis that insectivorous birds are attracted to, and utilize, habitat disturbance. The foraging behavior that we observed is likely an extension of a pre-existing foraging behavior. We (as large mammals) were viewed not as a threat, but as agents of disturbance, providing insectivorous birds access to prey items. Small songbirds (order Passeriformes), such as those observed here, have co-existed with a diversity of large-bodied game birds and mammals, capable of disturbing the ground layer, for millions of years in the subtropical and temperate mountains of southern China, providing ample time and opportunity for interspecific foraging associations to evolve and persist. Given that we specifically cut and disturbed the bamboo understory, it is tempting to suggest that the recruitment behavior we observed possibly evolved in association with the Giant Panda (*Ailuropoda melanoleuca*), which is famously reliant on this food source and disturbs the bamboo understory as it forages (Sheldon 1937; Johnson et al. 1988). It is possible that the observed behavior evolved in association with the Giant Panda during the past millennia when the species was widespread in the mountains and lowlands of central and southern China (Loucks et al. 2001).

The recruitment of birds to our disturbance may be an extension of foraging associations with particular large-bodied species, general associations with the collective suite of larger animals that occur in the region, or a more general attraction to any active forest disturbance, including landslides, tree falls, or edges of fires. It is most plausible that this foraging strategy is not species specific, but has rather evolved in association with general disturbance and high diversity of pheasants and large mammals in the region. If this foraging behavior evolved in association with a suite of large-bodied animals and/or general disturbance, this might explain the ease with which the birds exploited our disturbance in the forest. Thus, the foraging behavior that we observed may naturally extend from a pre-existing adaptive foraging strategy rather than represent a stark modification of behavior.

Of the birds that we observed foraging in the cleared net lanes, all the species are insectivores and predominately forage for insects and larvae on the ground and in low vegetation (del Hoyo et al. 2005). For example, species like Gould's Shortwing (*Heteroxenicus stellate*) are largely terrestrial. The species that we observed foraging the most extensively in the disturbed areas (the shortwing and the two *Tarsiger* bush-robin species) belong to the same family (Muscicapidae) as the European Robin. It is unknown whether these species independently evolved this foraging

strategy or if this behavior is ancestral in muscicapids. Variation in the strength of human associations among European Robin populations suggests that this adaptive foraging strategy may be easily lost and gained (Lack 1948). A detailed study of the geographic and taxonomic extent of this adaptive foraging strategy would increase our understanding of the evolutionary and ecological context of this behavior.

At middle and upper elevations in the mountains of southern China the ground is covered in snow for large portions of the year. In response, the majority of insectivorous birds migrate to lower elevations for the winter to escape cold temperatures and a lack of resources at upper elevations (del Hoyo et al. 2005). When these birds return to breeding elevations in March and April the ground can still be covered in snow, with the possibility of additional snow accumulation (Fig. 1). It is possible that disturbance from pheasants and large mammals may contribute to the survival of insectivorous birds at upper elevations during periods of snow cover when invertebrate prey items are otherwise trapped beneath the snow layer. Lack (1948) noted that European Robins were more likely to be associated with humans in winter. He hypothesized that the strength of foraging associations fluctuates among seasons in response to resource availability. Seasonal variation in resource availability in the mountains of southern China may explain the difference we observed in the strength of response to disturbance between our initial observations and the experiment. The recruitment response to disturbance appeared weaker in mid-July (during the experiment) than it did 1.5 months earlier when we made our initial observations. For example, in early May we observed multiple individuals foraging in net lanes at the same time, and birds foraged while bamboo was being cut, neither of which occurred during the experiments in mid-June. Additionally, only three of the eight individual birds that we observed in the disturbance treatment foraged extensively in the cleared areas. Our observations are consistent with Lack's (1948) seasonal observations in the European Robin, suggesting that seasonal resource fluctuations may regulate the strength of adaptive foraging associations through the year.

Additional explanations for the apparent difference in the response strength between our initial observations and the experiment include decreased density and mobility of birds in mid-June around 3000-m elevation. In early May (when our initial observations were made) the community is more dynamic and birds are more likely to cross paths with larger animals; birds are establishing breeding territories, females are finding mates, and a portion of the community at 3000-m elevation is migrating upslope. These dynamics are exemplified in our initial observation of two adult male *T. chrysaeus* foraging together in a

cleared net lane, an unlikely scenario once breeding territories are set. By mid-June, breeding territories are established, spring migration is complete, and birds are nesting, decreasing the density of birds foraging in the environment at a given time. Our results and observations are consistent with the hypothesis that insectivorous birds may be more reliant on interspecific foraging strategies during migration and in early spring when resources are scarcer at upper elevations, but this seasonal dynamic warrants further investigation.

In this study we provide observational and experimental evidence that multiple insectivorous bird species are attracted to human disturbance in primary subalpine forest, where they gain foraging opportunities. The observed birds conspicuously and extensively foraged in the disturbed area, often responding within minutes of our initial disturbance. The ability to exploit novel foraging opportunities, specifically in association with humans, highlights behavioral flexibility within a bird community that experiences relatively little human disturbance. The relative speed and ability of birds to exploit novel foraging opportunities by coopting pre-existing interspecific associations could potentially facilitate species survival in the wake of environmental change and shifts in community composition, especially as humans increasingly modify the environment (Walther et al. 2002). Our observation that human disturbance provided foraging opportunities for birds in primary forest offers a promising direction for future research at the interface of adaptive behavior, environmental change, conservation biology, and biodiversity science.

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