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Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice

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In mixed-species foraging flocks of forest birds, one or a few nuclear species frequently produce alarm calls and are followed by other species in the flock. We tested the hypothesis that similar asymmetries may exist in a second interspecific social context, multispecies mobbing behaviour. We examined mobbing behaviour evoked by an eastern screech-owl, *Megascops asio*, model and playback in two nuclear species, Carolina chickadees, *Poecile carolinensis*, and tufted titmice, *Baeolophus bicolor*, and in a species that follows them, the white-breasted nuthatch, *Sitta carolinensis*. Asymmetries in mobbing were not the same as those in mixed-species flocks. Nuthatches and chickadees mobbed with greater frequency and intensity compared to titmice, which remained at greater distances from the owl model and vocalized less frequently. We also tested for the existence and nature of potential interspecific vocal information flow during mobbing. Chickadee and nuthatch calling rates were positively correlated, as were chickadee and titmouse calling rates. Nuthatches and titmice rarely mobbed simultaneously. These results suggest the existence of positive feedback among species' mobbing intensity during a multispecies mobbing association as opposed to heterospecific vocal interference or a lack of heterospecific influence. However, randomization simulations showed that this positive feedback was not driven by a particular 'nuclear' species during mobbing, suggesting that the correlations may result from a mutually interdependent escalation of mobbing intensity.

Acoustic alarm signals that function adaptively to communicate with conspecifics and predators are often available in the public domain, allowing other species the opportunity to detect and benefit through adaptive responses to these signals (Shier 2002). Many mammals and birds have learned to associate heterospecific alarm calls with the presence of a predator (Hauser 1988; Shriner 1998; Fichtel 2004; Rainey et al. 2004; Magrath et al. 2007). The nature and directionality of vocal antipredator information flow among species is particularly relevant to species involved in interspecific social foraging groups. The benefits of interspecific sociality may, in fact, be linked to the complementary information provided by heterospecifics about different species of predators (Rasa 1983; Zuberbühler 2000). Avian mixed-species foraging flocks are a complex case of potential vocal information transfer, as they often contain large numbers of species. The diverse antipredator responses of heterospecifics in such flocks may have an additive effect on the information available as a consequence of flock membership (Goodale & Kotagama 2005a).

In mixed-species bird flocks, alarm calls are given by flock members in response to predators that represent immediate and usually extreme risk of predation (Ficken & Witkin 1977). The response to these alarm calls is for all birds in the flock to immediately stop movement and produce vocalizations for several minutes, and the first loud calls by flock members signal a return to activity (Morse 1973; Gaddis 1980; Sullivan 1984). Previous research has identified particular 'leader' and 'follower' species types in most avian mixed-species foraging flocks, termed 'nuclear' and 'satellite' species, respectively (Moynihan 1962; Morse 1977; Greig-Smith 1978; Diamond 1981; Munn 1984; Goodale & Kotagama 2005b). Nuclear species typically give frequent vocalizations, including alarm calls, or occur in large, active conspecific social groups, or both (Greenberg 2000). Satellite species often occur singly or in pairs and follow the nuclear species in the flock (Munn 1985). Vocal information about the presence of aerial predators typically flows from the nuclear species to the satellites (Munn & Terborgh 1979), although vocal information flow between multiple nuclear species also occurs (Goodale & Kotagama 2008).

The typical nuclear–satellite behavioural asymmetry can be observed in the forest flocks of eastern temperate North America where Carolina chickadees, *Poecile carolinensis*, tufted titmice,

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Baeolophus bicolor, and white-breasted nuthatches, *Sitta carolinensis*, co-occur in interspecific social-foraging groups during the nonbreeding season. Chickadees and titmice, the nuclear species, are often followed by many satellite species, principally woodpeckers and nuthatches (Morse 1970; Berner & Grubb 1985; Dolby & Grubb 1999). White-breasted nuthatches reduce vigilance and increase foraging rates when chickadees and titmice are present (Dolby & Grubb 1998). Observational and experimental evidence suggests that satellite species respond evasively to the aerial predator alarm calls of chickadees and titmice as described above (Gaddis 1980; Sullivan 1984).

Chickadees, titmice and nuthatches also interact in a context other than that of the mixed-species foraging flock. Small forest birds (chickadee = 10 g, titmouse = 21 g, nuthatch = 21 g) commonly show simultaneous mobbing behaviour towards small owls, such as pygmy-owls in western North America (Nocedal & Ficken 1998; Deppe et al. 2003; Templeton et al. 2005) and eastern screech-owls, *Megascops asio*, in eastern temperate woodlands (McPherson 1981; Gehlbach 1994; Gehlbach & Leverett 1995). The formation of a mobbing group is typically initiated by vocalizations with broadband frequency, rapid onset and high delivery rate (Marler 1955; Curio 1978; Klump & Shalter 1984). Unlike responses to alarm calls in foraging flocks, these mobbing associations are active and relatively noisy interactions with a less extreme threat than is present for the alarm calls described above (Curio 1978). In mobbing associations, the flock tries to drive the predator away from a given area. Eastern screech-owls are sit-and-wait predators of adult birds during the early morning and late evening hours (Gehlbach 1994) and so may be vulnerable to disturbance from mobbing birds during the day.

Directionality of Potential Vocal Information Flow

Here, we address two previously unexamined aspects of the multispecies mobbing behaviour of small woodland birds. Our first hypothesis was that the directionality of interspecific information flow is consistent across two behavioural contexts, the mixed-species foraging flock and multispecies mobbing association. We analysed the order of species' responses during the onset of a mob and species' vocal contributions during multispecies mobbing. If the foraging flock pattern of vocal antipredator information flow from nuclear flocking species to satellite species is maintained during predator mobbing associations, we predicted that chickadees and titmice would play a central role in maintaining the multispecies mob. In fact, there is some evidence of a 'nuclear' role of chickadees and titmice in mobbing associations. Heterospecifics show mobbing behaviours in response to chickadee and titmouse mobbing calls (Hurd 1996; Turcotte & Desrochers 2002; Sieving et al. 2004; Betts et al. 2005; Templeton & Greene 2007).

Interspecific Interactions during the Mobbing Association

The dynamics of species' interactions during multispecies mobbing behaviour are unknown. Several experimental studies (Vieth et al. 1980; Hurd 1996; Forsman & Mönkkönen 2001; Templeton & Greene 2007) have shown that mobbing calls stimulate mobbing behaviour in heterospecifics (Altmann 1956; Latimer 1977; Ficken & Popp 1996). However, natural interspecific interactions during mobbing have not been quantified. Our second hypothesis was based on an analysis of natural temporal patterns of these species' mobbing calls within a bout of mobbing. We hypothesized that escalation of mobbing intensity in conjunction with heterospecifics would be favoured over a strategy of independent escalation. Coordination of mobbing intensity among small prey species would be beneficial if successful interference with a predator's hunting success (Pettifor 1990; Flasskamp 1994; Deppe et al. 2003; Sunde et al. 2003; Hendrichsen et al. 2006) requires large amounts of noise. Chorusing may also mitigate the risk of mobbing itself or the predation risk associated with mobbing calls (Krama & Krams 2005). Ficken (1989) hypothesized that the apparently clumped patterns of conspecific calls in mobbing black-capped chickadees may prevent a predator from localizing individual callers. If escalation of the mob is contingent upon the behaviour of heterospecifics, species' calling rates should be positively correlated. Alternatively, heterospecific calling may interfere with conspecific communication (Brumm 2006; Planque & Slabberkoorn 2008). If such interference occurs during mobbing, negative correlations among species' calling rates are expected.

Asymmetries in vocal information flow may also occur within the mobbing chorus. If mobbing behaviours of all species have equal relevance to mobbing heterospecifics, then changes in the calling rate of any given species may result in coincident changes in the calling rate of heterospecifics in an interspecific mobbing chorus. Alternatively, particular species may have greater influence on the mobbing intensity of heterospecifics. In particular, chickadees and titmice may play a 'nuclear species' role in mobbing. If so, then nuthatch mobbing vocalizations and behaviour should be dependent upon chickadee and titmouse mobbing behaviours. Evidence of this asymmetry may exist at the level of individual mobbing calls such that nuthatches would be more likely to call immediately after a chickadee or titmouse call.

METHODS

This research was conducted at Purdue University's 160 acre Ross Biological Reserve and in the adjacent Ross Hills County Park located along the Wabash River in west-central Indiana, U.S.A. Forest type varies from dry oak–hickory ridge-tops, to maple–tulip poplar slopes and bottomland cottonwood–sycamore along the river. The entire reserve is marked with a 40 × 40 m colour-coded grid and covered by an extensive trail system.

The data analysed here were collected during playback experiments conducted between September 2005 and July 2006. Playbacks in September and October 2005 consisted of eastern screech-owl monotonic trills for a period of 10 min. Winter 2006 playback consisted of eastern screech-owl monotonic trills in combination with chickadee, titmouse or nuthatch mobbing calls for a period of 6 min. Otherwise, the 2005 and 2006 playback procedures were identical. A screech-owl model was placed near the trunk of a small tree approximately 2 m from the ground to provide a visual stimulus for mobbing behaviour. Mobbing birds focused attacks towards the model, often swooping towards it and occasionally making physical contact. The use of predator playback in conjunction with a model mimics the natural predator–prey interaction because passerines often mob calling screech-owls. In fact, the playback of screech-owl calls alone will evoke mobbing behaviour (McPherson 1981). The use of predator playback also ensured that all individuals in hearing range had the opportunity to simultaneously become aware of the owl.

This study was approved by the Purdue Animal Care and Use Committee (protocol no. 04-083). Birds resumed normal foraging activity immediately after the end of playback and usually left the area, sometimes before the playback ended. Overall disturbance from the predator playbacks was also minimal because successive playbacks at the same site were separated by at least 7 days to minimize habituation.

Playbacks were conducted using a Saul Mineroff amplified field speaker attached to the tree just below the owl model, a Sony Walkman CD player, and 12 m of speaker cable for remote initiation