CULTURAL BREAKDOWN OF LEARNED AVIAN ALARM CALLS: IMPLICATIONS TO MANAGEMENT AND CONSERVATION

by

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Cultural breakdown of learned avian alarm calls: implications to management and conservation

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Abstract

Mobbing is a common response of prey birds to aggressively displace potential predatory birds. This behavior transcends lineages and empirical evidence indicates that auditory cues from one species elicit mobbing responses in the same and/or different species. The black-capped chickadee (*Pocile atricapillus*) varies the number and length of D notes in the "chick-a-dee" mobbing call to denote information about the threat level a potential predator poses, with more numerous, shorter D notes designating a high threat. However, their limited natal dispersal may result in restricted transmission of culturally important vocalizations, which are known to quickly diminish in songbird populations that become isolated or are small in size, potentially exacerbating their decline. Whereas the black-capped chickadee and associated mixed flock members are common, we use this system as a model to study the cultural transmission of information important to prey survivorship and as a model of cultural breakdown in bird populations that are threatened by isolation. This project was replicated in areas containing persistent populations of Eastern screech owls (*Megascops asio*) and in those historically lacking them to assess whether black-capped chickadee alarm calls have a site-specific learned cultural component. Regional dialects are not hard-wired but learned in many songbirds, and locale-specific calls may uniquely convey information to members of the same mixed flock. Our data show that "chick-a-dee" warning calls differ in response to eastern screech owl presence. Where black-capped chickadees co-occurred with eastern screech owls, the average number of D notes was 5.25 but in areas lacking them, the average number of D notes was 2.25. Moreover, the length of the first D note was 40% shorter in areas with a persistent screech owl population. This indicates a breakdown in their vocal culture and suggests management that increases the connectivity of otherwise isolated populations can be of strong conservation value to many songbirds in decline.

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Introduction

Many animals produce variable alarm calls in response to the threat level of a potential predator (Seyfarth et al. 1980; Templeton et al. 2005). These calls often elicit recruitment of individuals to harass predators out of the area via mobbing (Hurd 1996; Templeton & Greene 2007) and are known to contain very specific information important to prey survivorship such as predator type, location or level of threat. For example, vervet monkeys (*Chlorocebus aethiops*) give different alarm calls for leopards, eagles and snakes (Seyfarth et al. 1980), white-browed scrubwren (*Sericornis frontalis*) produce variable flee alarm calls based on aerial predator distance (Leavesley & Magrath 2005) and black-capped chickadees (*Poecile atricapillus*) give a gradient of different alarm calls which designate the risk level of predation (Templeton et al. 2005). Although these alarm calls are often aimed at conspecifics, they can be learned by heterospecifics as well and elicit a mixed flock mobbing response via eavesdropping, which can lower predation risk for all flock members (Templeton & Greene 2007; Lea et al. 2008; Schmidt et al. 2008).

Some antipredator behavior is hard wired and individuals exhibit an avoidance response despite no prior experience with particular predators (Cross 1978; Csányi 1985). However, in many songbirds, alarm call structures are learned (Beecher & Brenowitz 2005; Fitch 2009) and thus are expected to be spatially and temporally dynamic as predator abundance and composition change in space as well as over generations of prey (Griffin 2004). This cultural learning can result in antipredator behavior that is locale-specific (Lima & Dill 1990). Moreover, if predators are absent from an area for one or more songbird generations, this may affect the learned alarm call structures and thus compromise prey survivorship if prey in that population are exposed to particular predators in the future. Culturally transmitted communications like the song repertoire and territorial calls are known to diminish in isolated songbird populations, potentially exacerbating to their decline as important vocalizations are lost (Laiolo & Tella 2005; Laiolo & Tella 2008; Briefer et al. 2010; Rivera-Gutierrez et al. 2010).

The black-capped chickadee (*Poecile atricapillus*), a small non-migratory songbird, is widespread and common throughout its North American range. They produce a loud broadband "chick-a-dee" call in response to a perched predator used to recruit other birds to mob and a high pitched "seet" in response to an aerial predator that causes individuals to freeze or take cover (Smith 1991; Templeton & Greene 2007). During the non-breeding season, chickadees form mixed flocks with species that face many of the same predation risks (Smith 1991; Templeton & Greene 2007), and this affords heterospecifics an opportunity to eavesdrop on information important to survival. For example, Templeton and Green (2007) found that the red-breasted nuthatch (*Sitta canadensis*) responds appropriately to variations in "chick-a-dee" alarm calls for a great horned owl (*Bubo virginianus*; small threat) and a northern pygmy owl (*Glaucidium gnoma*; large threat). Templeton et al. (2005) also found the number of D notes given by chickadees positively correlates with the threat level a particular predator poses. Approximately 50 species are known to respond to "chick-a-dee" alarm calls and join in on the mobbing (Gunn et al. 2000).

Black-capped chickadees have a median natal dispersal distance of approximately 1.1 km (Weise & Meyer 1979), and in Northeast Ohio, eastern screech owls (*Megascops asio*) have historically been absent throughout regions much larger than this. However, some areas maintain a persistent high density (Randy Jones, Ray Novotny, local park managers, pers. comm.; Peterjohn 2001, also see results). In this study, we assessed whether a historic low abundance of the eastern screech owl, a small, dangerous predator of small songbirds, caused a breakdown in the transmission of alarm call information among populations of black-capped chickadees. Because screech owls are a large threat to black-capped chickadees and their patchy distribution may culturally isolate chickadee populations, we hypothesized that their historic absence would affect warning call information given by chickadees. To test this, we captured chickadees from areas with and without screech owls and analyzed components of the chickadee's warning call when presented with a screech owl model.

Whereas the black-capped chickadee is common, we use this system as a model to study the cultural transmission of information important to prey survivorship. Since important bird vocalizations can degrade quickly, they may become an early warning sign for detecting the deleterious effects of isolation over short periods of time (Laiolo & Tella 2005). If the transmission of alarm call structure declines with the absence of particular predators but may have future survivorship value, this suggests management which increases the connectivity of otherwise isolated populations can be of strong conservation value to many songbirds in decline.

Methods

Recording calls

Twelve black-capped chickadees were captured in Northeast Ohio from February through May 2011, including locations in Poland Township, Yellow Creek Park (Struthers), Mosquito Creek State Park (Cortland), Mill Creek Metro Parks (Youngstown), Berlin Lake (Berlin Center), and Beaver Creek State Park (East Liverpool). A federal fish and wildlife (USFWS) scientific collecting permit (#MB17155A-0) and an Ohio division of wildlife (ODNR) scientific collecting permit (#11-363) were obtained to capture the chickadees. The closest capture area with eastern screech owls to an area without them was 40 km. Given that median natal dispersal distance for chickadees is 1.1 km (Weise & Meyer 1979), this virtually insured that all captured chickadees had not dispersed between areas with/without screech owls. Chickadees were caught using a WCS Sparrow Sled (Copyright 2011 WCS, LLC) with an attached two-chambered hanging trap. Traps hung near feeding stations with six foot Shepard's hooks. After a chickadee was captured, the trap was covered with a sheet and the chickadee was allowed to calm down for five minutes. A Sennheiser shotgun microphone (model unknown) was placed on the trap. After the bird calmed down, the sheet was lifted and a mounted stuffed eastern screech owl located with 0.5 m of the trap was revealed (the owl was loaned from the Cleveland Museum of Natural History by Dr. Andy Jones). Alarm calls produced by the black-capped chickadee were recorded for ten minutes using a Marantz professional portable solid state recorder (model # PMD670) and then the chickadee was released.

Call and Statistical Analysis

Black-capped chickadee alarm calls were analyzed using Raven Lite software (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.). For a maximum of 10 minutes following the owl presentation, the number of calls and number of D notes per call were averaged for each individual and compared between groups (n=3 and n=9 individuals from areas with and without screech owls, respectively). We also analyzed the time between the "chick" and D notes and the duration of the first D note because these can differ based on predator threat level (Templeton et al. 2005; Soard & Ritchison 2009). For these factors, we used the first five clean calls that included both "chick" and D notes and averaged them for each individual.

All data were analyzed using a one-way ANOVA in SPSS (PASW Statistics 18, IBM®, 2009), with presence or absence of screech owls as treatment levels. Treatment variances were heterogeneous for the number of D notes ($p=0.042$) and number of calls ($p=0.011$, Levine's HOV test) and we present analysis from log-transformed data, which resulted in homogeneous variance ($p>0.05$). However, homogeneous treatment level variances were found for the other two factors and thus no other transformations were necessary ($p>0.05$). An a priori α-level was set at 0.05 for all statistical tests.

Owl Survey

Owl surveys were performed to assess if eastern screech owls were present in areas in which black-capped chickadees were captured. The methods were adapted from Takats et al. (2001). The surveys took place half an hour after sundown between November 2010 and April 2011, and each of the 8 sites were surveyed 1-2 times during this interval (also see below). The eastern screech owl calls were taken from A Field Guide to Bird Songs: Eastern and Central North America (Peterson Field Guides, 1990) and were played on a Foxpro Spitfire digital game call (model no. SF1). The volume was set so the owl call could not be heard by a human at 225m, with the assumption that an owl could not hear it at 400 m. Along an approximately 2 km transect, a one minute playback trail was conducted every 400 m followed by a one minute silent period. This was repeated four times in each cardinal directions at each sampling point (n=4-6 points per location). If no screech owl responded to the playback during any survey, we assumed screech owls were not present. Of note, our owl survey presence-absence data corroborated well with the personal communications of local park managers and the currently ongoing Ohio Breeding Bird Atlas II data.

Results

Call and Statistical Analysis

We recorded a total of 231 “chick-a-dee” alarm calls from 12 individuals. Black-capped chickadees from non-screech owl areas produced a total of 106 calls (n=9 individuals, mean =11.8 ±3.0 (SE)) while chickadees from screech owl areas produced 125 calls (n=3 individuals, mean=41.7±16.7). However, this 253% increase in call number was not quite significant because of high within-group variance ($F_{1,11}$=4.30, p=0.065; based on log-transformed data). Individuals from areas without and with screech owls respectively averaged 2.25 and 5.25 D notes per call. Using log-transformed data, we found the number of D notes produced in areas with eastern screech owls was significantly higher (133%) than in areas lacking them ($F_{1,11}$ = 7.54, p=0.021). The length of the first D note produced by chickadees in areas without screech owls was

67.5% longer than in areas with them ($F_{1,11}$=40.4, p<0.001). However, there was no significant difference in the length of time between the "chick" and the D notes between the two groups ($F_{1,11}$=0.06, p=0.816).

Owl Survey

Based on our surveys, eastern screech owls were only found at Beaver Creek State Park in East Liverpool. Within this area, chickadees were caught at a distance >1.5 km from one another to ensure that chickadees were from different flocks (Freeberg & Lucas 2002). There were no screech owls detected at any other site, which corroborates with the currently ongoing Ohio Breeding Bird Atlas II data as well as all local park managers and experienced ornithologists except for one site (Berlin Lake, Berlin Center).

Table 1					
Location	ESOW Present	# of Calls	# of D notes (avg.)	Length of 1st D note (s) [1]	Length between "chick" and D (s) [1]
Poland Township	No	32	2.34	0.160	0.036
Yellow Creek (office)	No	9	1.89	0.149	0.050
Yellow Creek	No	18	1.67	0.140	0.039
Mosquito (office)	No	12	3.42	0.141	0.046
Mosquito (Horse Trial)	No	6	2.00	0.137	0.049
Mill Creek (Ford Nature Center 1)	No	11	2.10	0.141	0.045
Mill Creek (Ford Nature Center 2)	No	2	2.00	0.171[2]	0.036[2]
Mill Creek (Boat House)	No	3	3.00	0.176[2]	0.045[2]
Berlin Lake	No	13	1.84	0.172	0.056
Beaver Creek (Education Center 1)	Yes	52	4.79	0.094	0.042
Beaver Creek (Education Center 2)	Yes	9	4.11	0.082	0.050
Beaver Creek (Park Office)	Yes	64	6.85	0.100	0.045

Variations in alarm call given by black-capped chickadees from each capture location
[1] = 1st 5 clean calls used [2] = individuals gave <5 calls so all calls used

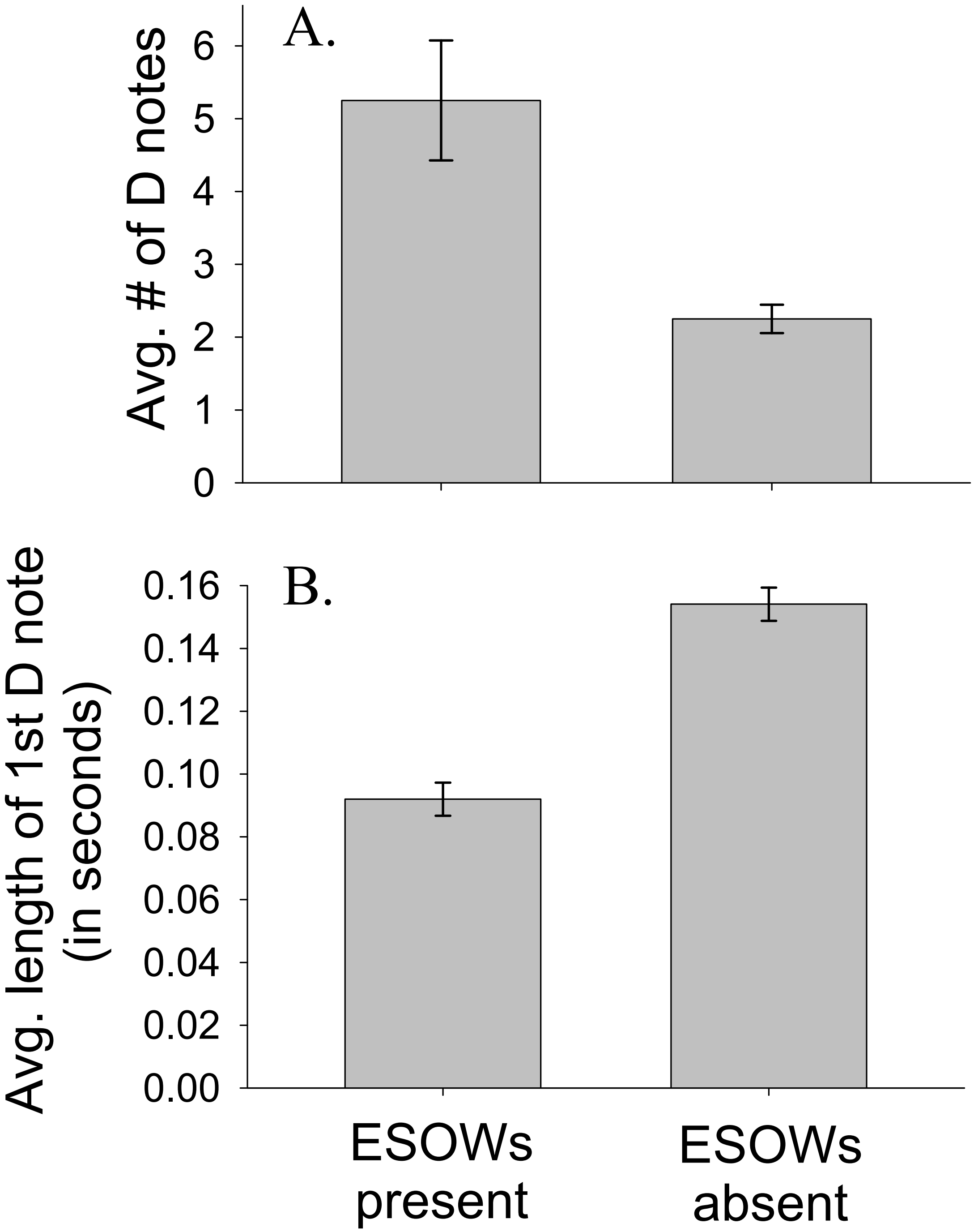

Figure 1: In areas where Eastern screech owls (ESOWs) are present and absent, the (A) average number of D notes and (B) average length of the first D note elicited by captured black-capped chickadees when presented with a stuffed ESOW model. Means ± 1 SE are presented.

Discussion

Faunal community structure is spatially and temporally dynamic, as predator composition and abundance change in space as well as over generations of prey (Griffin 2004). This raises a fundamental question as to whether absence of a historically sympatric predator results in loss of innate predator recognition or loss of culture-based alarm call vocalizations. Inherent predator properties often elicit innate antipredator responses in prey, such as displaying two black circles to prey (Coss 1978; Csányi 1985). This is particularly likely for continental species, as their ancestral lineages have periodically been subjected to numerous and different types of predators. In addition, according to the Multipredator Hypothesis, the presence of any phylogenetically similar predator is enough for prey to maintain antipredator behaviors for a currently absent but historically sympatric predator (Blumstein 2005).

Given this, it is unlikely that the differential alarm call structures produced by black-capped chickadees in areas with and without eastern screech owls were the result of a loss of predator recognition, but might rather have resulted from a breakdown in their culturally learned alarm call for eastern screech owls. Indeed, predator absence can cause a breakdown of culturally transmitted, experienced-based antipredator behaviors in as little as one generation (Blumstein et al. 2004). Moreover, black-capped chickadees still face many dangerous avian predators such as sharp-shinned (*Accipiter striatus*) and Cooper's hawks (*Accipiter cooperii*).

Culturally transmitted vocalizations are known to breakdown in many avian species when a population becomes isolated, and this can lead to a loss of information important to reproductive success and prey survivorship (Laiolo & Tella 2005; Laiolo & Tella 2008; Briefer et al. 2010; Rivera-Gutierrez et al. 2010). Our data suggest that in areas in Northeast Ohio lacking eastern screech owls, black-capped chickadees have lost components of their learned alarm call structure for eastern screech owls. Indeed, chickadees from Beaver Creek State Park, which harbors a healthy eastern screech owl population, elicited significantly shorter and more numerous D notes when exposed to a screech owl model and these factors are known to designate a high treat level (Figures 1 and 2, Templeton et al. 2005).

Observing mobbing behavior or a conspecific in trouble can act as a stimulus which causes predator avoidance learning (Kruuk 1976; Conover & Perito 1981; McLean et al. 1999; Griffin 2004). Predator recognition via cultural transmission has been demonstrated in European blackbirds (*Turdus merula*), which will mob a bird for which they were initially indifferent once they see a conspecific mob it (Curio et al. 1978; also see Chivers & Smith 1995; Mathis et al. 1996 for fathead minnow examples). This learned response can be passed between at least six conspecifics without a decline in their response. Threat-appropriate responses are also learned in red-breasted nuthatches (*Sitta canadensis*), which modulate their antipredator behavior based on variations in "chick-a-dee" alarm calls for a great horned owl (*Bubo virginianus*; small threat) and a northern pygmy owl (*Glaucidium gnoma*; large threat; Templeton & Green 2007). Given that black-capped chickadees do not elicit a threat-appropriate alarm call for eastern screech owls in areas lacking them, and thus there is no opportunity for conspecifics or heterospecifcs to learn a proper response, survivorship for all flock members may be compromised if prey in that population are later exposed to this predator.

Increasing interest is emerging for the need for culture and behavior to be integrated into management and conservation planning (Curio 1996; Anthony & Blumstein 2000; Ryan 2006; Laiolo & Tella 2008; Laiolo 2010). Any acoustic traits linked to recruitment, survivorship and reproductive success are significant to conservation because they can affect population growth rates (Briefer et al. 2010; Laiolo 2010; Rivera-Gutierrez et al. 2010). In many songbirds, this acoustic information, including antipredator behavior, is culturally transmitted and thus survivorship can be reduced if this information is disrupted (Rabin et al. 2006; Laiolo et al. 2007). Whereas the black-capped chickadee and associated flock members are common, we use this system as a model to study the breakdown of culturally transmitted information important to prey survivorship. Given that culturally transmitted communications like song repertoire and territorial calls are known to diminish in isolated songbird populations, which can exacerbate their decline as important vocalizations are lost (Laiolo & Tella 2005; Laiolo & Tella 2008; Briefer et al. 2010; Rivera-Gutierrez et al. 2010), this suggests management which increase the connectivity of otherwise culturally isolated populations can be of strong conservation value to many songbirds in decline.

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November 30, 2010

Dr. Ian Renne
Biology Department
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Re: IACUC Protocol # 05-10
Title: Cultural breakdown of avian mobbing response to the site-specific alarm calls: implications to management and conservation.

Dear Dr. Renne:

The Institutional Animal Care and Use Committee of Youngstown State University has reviewed the aforementioned protocol you submitted for consideration and determined it should be unconditionally approved for the period of November 30, 2010 through its expiration date of November 30, 2013.

This protocol is approved for a period of three years; however, it must be updated yearly via the submission of an Annual Review-Request to Use Animals form. These Annual Review forms must be submitted to the IACUC at least thirty days ***prior*** to the protocol's yearly anniversary dates of November 30, 2011 and November 30, 2012. If you do not submit the forms in a timely fashion, this protocol will be immediately suspended. You must adhere to the procedures described in your approved request; any modification of your project must first be authorized by the Institutional Animal Care and Use Committee. Good luck with your research.

Sincerely,

Dr. Peter J. Kasvinsky
Associate Provost for Research
Dean School of Graduate Studies and Research

PJK:dka

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