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Fuzzy clustering methods reveal structurally discrete and graded alarm calls in male Red-winged Blackbirds (*Agelaius phoeniceus*)

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ABSTRACT

Alarm calls, the vocalisations given during encounters with threats, vary tremendously in acoustic structure across species. Many alarm calls are structurally graded, which can convey information about predator type, urgency or proximity. However, graded variation is challenging to analyse with traditional categorical approaches. Here, we used fuzzy clustering to quantitatively classify and describe the alarm call repertoire of male Red-winged Blackbirds (*Agelaius phoeniceus*) in Michigan, U.S.A. We recorded calls from 74 males, generating a library of more than 13,000 vocalisations. We then selected 1,521 high-quality, non-overlapped calls for acoustic analysis and extracted 50 acoustic parameters per call. Using fuzzy k-means clustering, we identified the most stable number of call types, calculated membership values for primary and secondary clusters and developed thresholds that distinguish discrete, intermediate and graded call structures. Male Red-winged Blackbirds produced six alarm calls, *check, cluck, zeer*, *seee*, *se-er* and *ti-er*, which varied in the extent to which they share acoustic features. *Cluck* calls were discrete, whereas *zeer*, *seee*, *se-er* and *ti-er* formed a graded continuum; *check* calls were intermediate. These findings reveal previously unmeasured variation and unrecognised complexity in the species' alarm signalling system and demonstrate the value of fuzzy clustering for classifying graded vocal repertoires in animals.

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Acoustic structure; antipredator calls; call classification; graded signals; discrete signals; fuzzy clustering

Introduction

Across diverse taxa, animals give alarm calls that warn about imminent threats (Caro 2005). In some species, individuals produce discrete call types that appear to vary little in acoustic structure (Zuberbühler 2009; Gill and Bierema 2013). For example, meerkats (*Suricata suricatta*) produce six discrete sentinel calls that reflect different levels of predation risk and alter vigilance in this group-living species (Rauber and Manser

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2017). In other taxa, discrete calls are given predictably when confronting specific types of threats, such as in Yellow Warblers (*Setophaga petechia*) that use seet calls to denote brood parasitic Brown-headed Cowbirds (*Molothrus ater)* and give chip calls to nest predators and other intruders (Hobson and Sealy 1989; Gill and Sealy 1996, 2004; Lawson et al. 2021). In contrast to discrete calls, species may also produce structurally graded alarm calls that vary along one or more acoustic trait axes but that lack clear acoustic distinctions between call types (Zuberbühler 2009); graded alarm calls can vary in structure depending on external conditions, such as predation risk, or with the internal state of callers. For example, when confronted by closer, faster predators, domestic chickens (*Gallus gallus domesticus*) give calls that are shorter, more intense, more pure-toned and lower frequency compared with calls given to more distant predators (Wilson and Evans 2012). With extensive variation in structure, graded alarm calls offer signallers communicative flexibility and may encode a wealth of information about predation risk and social context (e.g. Fischer et al. 2001a, 2001b).

Although structural variation in graded alarm calls expands a species' communicative range, connecting antipredatory context with structural differences in graded signals can pose significant challenges for bioacoustic analyses. One approach treats graded signals similarly to discrete call types. In such an approach, 'hard' clustering techniques may be used, which forces each vocalisation into a distinct cluster. This forcing into distinct vocal categories may minimise or overlook meaningful variation within calls and may miss opportunities for deeper insights into the patterns of use, meaning and function of these signals (Fischer et al. 2017; Cusano et al. 2021). Accordingly, hard clustering is not well suited for call repertoires that include graded signals, which share acoustic features across clusters to varying degrees (Wadewitz et al. 2015). Alternative analytical techniques categorise graded signals and simultaneously quantify both within- and between-call variation in structure, providing greater insights into call repertoires. Fuzzy or 'soft' clustering allows for imperfect membership in multiple clusters such that graded signals share membership to varying degrees with all other clusters (Zadeh 1965; Bezdek 1981), making this approach more flexible and more appropriate for graded repertoires (Wadewitz et al. 2015; Fischer et al. 2017; Cusano et al. 2021). Metrics associated with soft clustering quantify shared membership and the strengths of association of calls with specific clusters, providing additional information with which to consider such graded vocal signals (Wadewitz et al. 2015; Fischer et al. 2017; Cusano et al. 2021).

We used fuzzy clustering to classify alarm calls given by male Red-winged Blackbirds (*Agelaius phoeniceus*). Red-winged Blackbirds (henceforth blackbirds) are widespread and extensively studied (Yasukawa and Searcy 2020) and fuzzy clustering provides an opportunity to revisit their known vocal complexity and vocal array or corpus, including documenting size of the alarm call repertoire and the nature of gradation within call types. The alarm call repertoire of male blackbirds has been estimated qualitatively as consisting of 7–8 alarm calls in several populations (Orians and Christman 1968; Beletsky et al. 1986), with 15–20 total calls possibly occurring in the species (Beletsky 1991). Some call types show considerable variability in acoustic structure and at least some variants appear to grade into others, as they are structurally similar to other alarm call types (Orians and Christman 1968; Yasukawa and Searcy 2020; K. Ray, personal observation). Here, we used fuzzy k-means cluster analysis (Ferraro and Giordani 2015; Wadewitz et al. 2015; Fischer et al. 2017), a type

of unsupervised clustering, on acoustic features to identify calls within the blackbird alarm call repertoire and quantify variation within calls. Our analysis quantitatively classifies call types and assesses within-call variation, thereby advancing the understanding of the blackbird vocal corpus and providing new perspectives on territorial males' alarm call system in this otherwise well-known species.

Methods

Study sites and species

We recorded unbanded male Red-winged Blackbirds between March and July 2022 at seven sites spanning mixed wetland and upland nature preserves in and around Kalamazoo, Michigan, USA. (42.2917° N, 85.5872° W). The preserves ranged in size from 12 to 284 ha and included public and private lands. When female blackbirds began nest building in early May, we focused our efforts at one study site, Sora Meadows Preserve (42.2342° N, 85.9343° W), to facilitate a concurrent study (K. Ray et al., unpubl.) during which we searched for and monitored nests to record vocalising males during known breeding stages. Sora Meadows Preserve is a reclaimed wetland (26.3 ha) consisting of wetland and upland habitat that supported a colony of 12–14 males and an estimated 25–30 female blackbirds.

Male blackbirds have a vocal system in which all territorial males within a colony call constantly throughout the breeding season, switching call types to communicate the presence of perceived threats (Beletsky et al. 1986). Termed 'alert' calls by Beletsky (1991), they may also be used in the absence of disturbance (Beletsky et al. 1986) and are also termed 'alarm' calls when predators are present (Orians and Christman 1968; Neudorf and Sealy 1992), with higher call and switching rates associated with closer or moving predators (Beletsky et al. 1986; Beletsky 1991). In this paper, we refer to these multi-use calls as alarm calls to be consistent with our other work in this system (Ray et al., unpublished data).

Recording male vocalisations

We aimed to describe and quantify the alarm call repertoire across male blackbirds, rather than explore individual differences in the use of these calls among males. Therefore, across seven sites, we recorded the vocalisations of an estimated 74 male blackbirds (~33 hr; excluding two additional males that did not give calls during our observations) over the breeding season to build an extensive library of male blackbird calls (n = 13,485), which we designate here as our full breeding season dataset. Males were unbanded and we systematically recorded them to minimise the possibility of resampling individuals. Specifically, when we located a focal male, we recorded him and his location; then, depending on the habitat of a particular study site, we moved 50–500 m to record the next male while keeping track of the previously recorded male(s). For wetland preserves other than our main study site, we visited each two times: once before and once after the arrival of female blackbirds. At Sora Meadows, males were typically recorded three times: after female blackbirds arrived and had settled on territories, at the egg stage and again at the nestling stage. We assumed we recorded the same males

across stages based on their territory location and the use of particular perches for singing.

We used Marantz solid-state digital recorders (PMD561; sampling rate of 44.1 kHz and bit rate of 16 bps) and Sennheiser shotgun microphones (MKH 70 P48) to record vocalisations of focal males from distances between 2 and 25 m. The distance at which we tracked blackbird males varied depending on how close we could approach them without apparently affecting their behaviour. Males sometimes moved away more than 25 m from us, but even at those distances, we continued to record them to quantify call rate and other behaviours for the concurrent study; however, we did not use these distant recordings in our acoustic analyses. K.A.R. and K.S.M. recorded and observed most males, with additional recordings made by E. Branch and J. Sblendorio.

Call feature extraction

We used Avisoft SASLab-Pro (Specht 2017) to generate spectrograms (FFT length of 512, frame size 100%, FlatTop window and temporal resolution overlap of 93.75%), from which we visually and aurally identified male blackbird calls (full breeding season dataset, $n = 74$ males, $n = 13{,}485$ calls). Two observers trained in bioacoustics (K.A.R. and K.S.M.) preliminarily labelled calls with 12 call names both defined in the literature describing blackbird vocal repertoires (Orians and Christman 1968; Beletsky et al. 1986), as well as those that did not fit published descriptions. Then, we identified a subset of high-quality and high-fidelity call recordings that were not overlapped by other vocalisations, wind or anthropogenic noise and extracted acoustic features using the automated parameter measurement tool (threshold ±15 dB) to create an 'acoustic features' dataset ($n = 1{,}521$ calls, $n = 46$ males). For pure tone, high-frequency calls only, a bandpass filter of 2–10 kHz was applied to remove low-frequency noise before analysis. Wadewitz et al. (2015) demonstrated that more accurate fuzzy clustering results occurred when a larger number of acoustic variables were included in analyses; therefore, we extracted 50 measurements per call for analysis (Supplementary Materials, Tables S1 and S2). Moreover, Wadewitz et al. (2015) found that applying fuzzy clustering after data reduction (factor analysis) inflated the number of call types in their study species relative to fuzzy clustering performed on acoustic features themselves as well as by expert classification. We focused on male alarm calls only and excluded male song, female calls (*scream*), rare call types (*growl*), pre-copulatory vocalisations (*ti-ti-ti*), the flight call complex (*pook*, *see-chuck*, *tlick*) and call types associated with migratory flocking behaviour (*slee*, *pit*; Orians and Christman 1968) in analyses.

Fuzzy clustering analysis

To classify alarm calls in the acoustic features dataset ($n = 1{,}521$ calls), we applied fuzzy k-means clustering (FKM; Ferraro and Giordani 2015; Wadewitz et al. 2015; Fischer et al. 2017) to the set of 50 acoustic features extracted for each call (Supplementary Materials, Tables S1 and S2). We ran FKM in R (v. 3.2) using the *wrapFKM* function in the *DoTC* package (Wadewitz et al. 2015) and the *FKM* function within the *fclust* package (Ferraro and Giordani 2015; Ferraro et al. 2019). We ran multiple rounds of FKM with varying levels of fuzziness ($\mu = 1.3$–2.6): a μ of 1 is equivalent to a hard k-means cluster, and as μ

increases in value, fuzziness between clusters increases (Bezdek 1981). The maximum number of clusters, k, was set to 15, which was above the 12-cluster solution based on our tentative labelling of calls and the maximum number of alarm calls identified by Orians and Christman (1968) and Beletskey et al. (1986).

To identify the optimal number of clusters in our dataset, we used a combination of evidence. First, as we increased the value of μ from the starting value of 1 (equivalent to hard clustering), we identified values of k that remained relatively stable (Wadewitz et al. 2015; Fischer et al. 2017; Supplemental Materials, Figure S1) and that were also biologically meaningful based on the literature. For example, as μ increases, fuzzy clustering can stabilise at low, and unrealistic, numbers of possible clusters (i.e. $k < 4$ here, which is lower than the number of described call types in the literature). Next, we examined internal cluster validation metrics provided by *fclust* for the three stable and biologically meaningful cluster solutions of 6, 9 and 11 call types (Ferraro and Giordani 2015; Ferraro et al. 2019) to identify the final cluster solution. We named each cluster based on our perception of the sound of the calls within the cluster, adopting call names used in the literature as appropriate. Finally, we compared call types identified by this analysis to spectrograms of calls in the literature to align call classifications (Orians and Christman 1968; Beletsky et al. 1986).

FKM analysis calculates metrics that reflect the extent of discreteness versus gradation in call structure. First, we generated membership values per individual call using FKM. In hard k-means clustering, membership values are binary, either 1 or 0; an individual call belongs to a cluster (1) or it does not (0). In FKM, each call receives a continuous membership value for each cluster identified in the stable model solution, with the sum of all membership values for a call equalling 1. Therefore, calls may belong to multiple clusters, with the highest membership value indicating the primary cluster to which a call belongs and membership values decreasing across remaining clusters. Note that although higher order membership values (e.g. tertiary values) were calculated, we present primary and secondary membership values only.

Using primary and secondary membership values, we next calculated typicality coefficients (TC) for individual calls (d). TCs were calculated by subtracting the secondary membership value from the primary membership value for each call (Wadewitz et al. 2015; Fischer et al. 2017). Calls with large TC values (i.e. d closer to 1) indicate that the call is more discrete. Conversely, individual calls with d approaching 0 indicate that a call is more graded. We also calculated mean TC values within clusters, and as with individual calls, clusters with mean TC values closer to 1 are more discrete and the spread of TC values within each cluster reveals which clusters tended to be more discrete than graded on average. The halved mean absolute deviation (Δ) from the average TC across all calls (d) was used to define a typicality threshold for the dataset (Wadewitz et al. 2015; Fischer et al. 2017). The typicality threshold consists of two cut-off values (reflecting positive ($d + \Delta$) and negative ($d - \Delta$) deviations from the mean) that are used to classify calls as discrete or graded; typical or discrete calls fall above the higher threshold value atypical or graded calls fall below the lower threshold value (Wadewitz et al. 2015; Fischer et al. 2017; Cusano et al. 2021).

The acoustic features dataset holds a fraction of the number of calls recorded in the full breeding season dataset. To expand our understanding of call usage by blackbird males, K.A.R. used a combination of the mean traits of call features from the acoustic features

Table 1. Mean (± SD) values of call duration and acoustic measurements taken at mean amplitude of male Red-winged Blackbird call types identified by fuzzy clustering. Means were calculated using the acoustic features dataset ($n = 1{,}521$ calls, $n = 46$ males), which included high-quality calls only. Definitions of acoustic parameters are provided in Table S2.

	Call type					
	Check	Cluck	Zeer	Seee	Se-er	Ti-er
Parameter	($n = 598$)	($n = 277$)	($n = 216$)	($n = 128$)	($n = 184$)	($n = 118$)
Duration (s)	0.069 ± 0.065	0.038 ± 0.015	0.393 ± 0.085	0.426 ± 0.140	0.383 ± 0.069	0.365 ± 0.062
Peak (Hz)	4100 ± 638.7	2611 ± 327.9	3871 ± 325.7	4655 ± 585.5	4044 ± 318.4	5223 ± 281.8
Min (Hz)	1293 ± 581.9	1677 ± 566.2	3414 ± 339.9	4187 ± 583.7	3625 ± 316.7	4834 ± 301.6
Max (Hz)	5718 ± 680.9	3398 ± 411.9	4932 ± 477.6	5955 ± 957.6	4923 ± 406.2	6444 ± 392.9
Bandwidth (Hz)	4418 ± 950.2	1717 ± 844.3	1512 ± 615.4	1762 ± 1413	1292 ± 512.9	1603 ± 512.5
Quartile 25 (Hz)	3124 ± 387.8	2256 ± 269.2	3847 ± 281.3	4577 ± 473.0	4018 ± 280.5	5163 ± 272.3
Quartile 50 (Hz)	4080 ± 348.2	2654 ± 216.1	4116 ± 226.2	4858 ± 298.2	4250 ± 227.8	5373 ± 204.6
Quartile 75 (Hz)	4846 ± 470.2	2988 ± 295.4	4628 ± 315.8	5488 ± 665.3	4712 ± 270.9	5719 ± 257.5

dataset (Table 1) and audiovisual inspection of spectrograms to classify the calls in the full breeding season dataset ($n = 13{,}485$ calls). As with the acoustic dataset, additional filters were applied to high-pitched calls in the full breeding season dataset to estimate the call features without low-frequency noise. When the calls were overlapped by other sounds that could affect the values of extracted acoustic features, we visually inspected spectrograms to classify calls. In some cases, the high-quality calls in the acoustic features dataset occurred within sequences of the same call repeated many times throughout the recording, which helped us to classify call types of lower quality calls in the full breeding season dataset (call type was then applied to the others in the call sequence). Although classifying by spectrograms was somewhat subjective, this process enabled us to generate a more complete picture of call type usage by naturally calling male blackbirds within our study population.

Results

Identifying call types in male Red-winged Blackbirds

The fuzzy k-means (FKM) cluster analysis of the acoustic features dataset ($n = 1{,}521$ calls, $n = 46$ males) first determined cluster stabilisation at the 11, 9 and 6 clusters solution, between a μ of 1.75 and 2.05 (Supplemental Materials, Figure S1). Of the three stable cluster solutions, the six cluster solution maximised internal validation metrics with a moderate fuzziness parameter ($\mu = 2.05$; Supplemental Materials, Tables S3 and S4) and produced a biologically meaningful number of calls based on prior knowledge of the system (Orians and Christman 1968). Based on our perception of the sound of these calls and existing names in the literature, we named these clusters *check* ($n = 598$ calls), *cluck* ($n = 277$), *zeer* ($n = 216$), *seee* ($n = 128$), *se-er* ($n = 184$) and *ti-er* ($n = 118$); we illustrate these clusters with high membership examples in Figure 1 (from left to right: *check, cluck, zeer, seee, se-er, ti-er*).

The numbers of assigned calls and their acoustic features varied across clusters (Table 1). The *check* and *cluck* clusters consisted of the shortest duration calls, and *zeer, seee, se-er* and *ti-er* were the longest. *Cluck* had the lowest peak frequency overall, and *ti-er* with the highest, with *check, zeer*, and *se-er*, intermediate between the extremes.

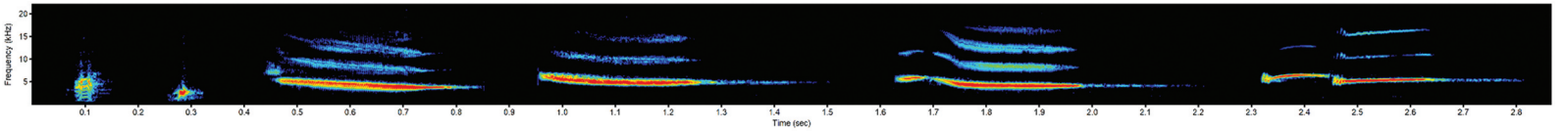

Figure 1. Examples of male Red-winged Blackbird calls in the six call clusters (from left to right: *check, cluck*, *zeer, seee, se-er* and *ti-er*) identified by fuzzy clustering. The selected calls showed high primary membership within their respective clusters.

The *check* cluster was more variable in peak frequency and had a wider range of values between minimum and maximum frequency than all other calls; *checks* are broadband, highly variable sounds. The *se-er* and *ti-er* clusters generally sounded disyllabic compared with the slurred sounds of *seee* and *zeer* clusters (Table 1). *Zeer* and *seee*, while somewhat similar visually, differ in noisiness, with *zeer* being much harsher and generally ending at a lower frequency and *seee* being a more pure tone sound.

The fuzzy relationships between call clusters

Membership values calculated per call reveal the primary cluster membership, as well as gradedness of a given call where a value of 1 means that a call fits only within a single call cluster. Primary membership values per call ranged from 0.192 to 0.970 across call clusters (Table 2), reflecting that all calls had memberships with more than one call cluster. Mean primary membership values per cluster, calculated from values of the individual calls, differed across call clusters and ranged from 0.359 to 0.779 (Table 2). The *cluck* cluster exhibited the highest mean primary membership value (0.779), indicating that most calls within *cluck* shared acoustic features primarily with other calls in this cluster (i.e. relatively discrete). In contrast, *seee* and *zeer* had the lowest mean primary membership values (0.336 and 0.359, respectively), revealing that calls within these call clusters shared acoustic features with multiple call clusters in addition to their primary assignment (i.e. relatively graded). The *check*, *se-er* and *ti-er* clusters had mean primary membership values near 0.5 (i.e. intermediate) (Table 2).

Secondary membership values reveal the call cluster to which individual calls have the next strongest fit (Supplementary Materials, Table S5). We plotted primary and secondary membership values for each call, which illustrates relationships in membership values between call clusters (Figure 2). Plots for some call cluster combinations (e.g. *ti-er/zeer* and *ti-er/se-er*) are absent because these cluster combinations did not contain calls that shared secondary membership with the other cluster. Membership plots with values concentrated along the dashed diagonal line point to shared acoustic features between call types; conversely, plots with more membership values closer to 1 on each axis reveal calls with more unique acoustic features relative to the second cluster.

Due to the nature of the fuzzy clustering analysis, calls in a given cluster likely share secondary membership values with another call cluster; however, the strength of the relationships varies with the relative membership values of calls

Table 2. Mean (± SD) primary membership values per primary call cluster assignment. Minimum and maximum values are the calls with the lowest and highest primary membership values for calls within a given call cluster. Higher mean membership values indicate call clusters that are less like other call clusters, compared with lower mean values, which indicate call clusters share features with other call clusters.

Assignment	Membership value	Minimum	Maximum	n
Check	0.493 ± 0.12	0.192	0.755	598
Cluck	0.779 ± 0.16	0.250	0.970	277
Zeer	0.359 ± 0.06	0.209	0.511	216
Seee	0.336 ± 0.08	0.193	0.530	128
Se-er	0.453 ± 0.13	0.232	0.715	184
Ti-er	0.471 ± 0.16	0.193	0.811	118

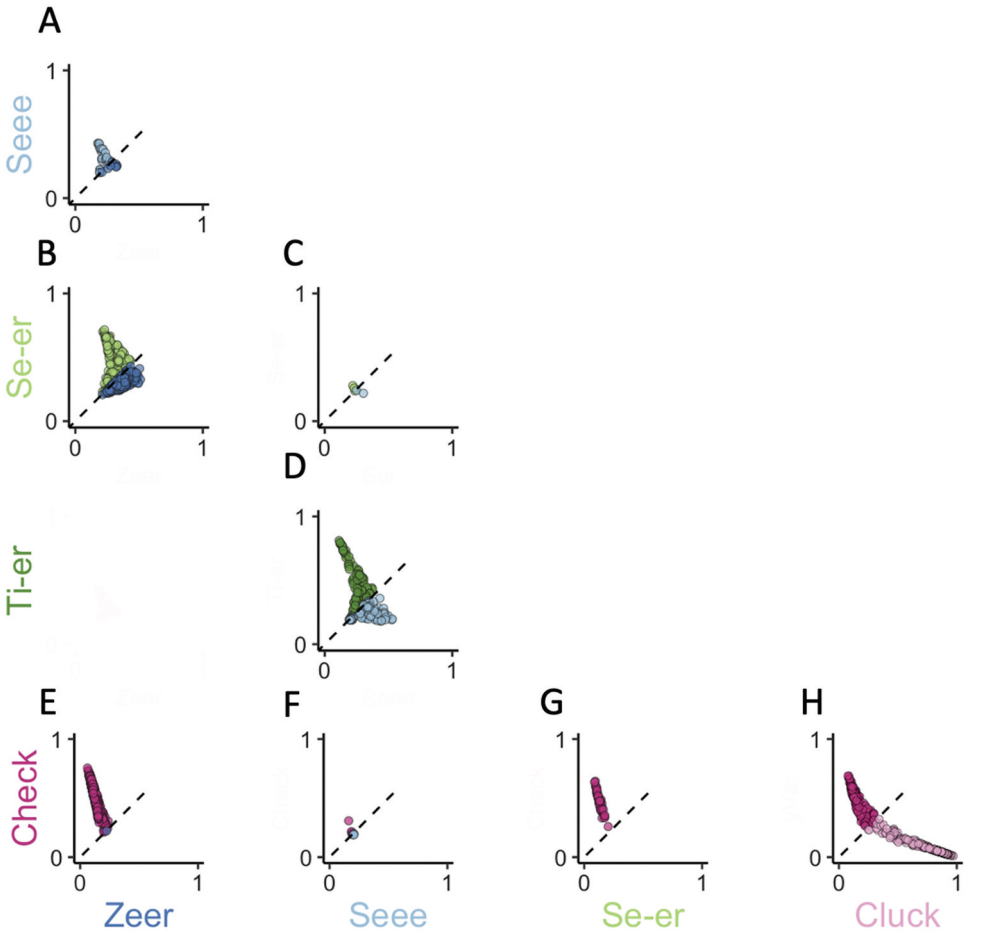

Figure 2. Primary and secondary membership plots of individual calls by call cluster: *check* (dark-pink), *cluck* (light-pink), *zeer* (dark-blue), *seee* (light-blue), *se-er* (light-green) and *ti-er* (dark-green). Calls are plotted by their first and second highest cluster membership values, such that each call is shown once ($n = 1{,}521$ calls). Calls on the dotted diagonal line have identical membership values in each respective call cluster and are more atypical within their call cluster type; calls closer to 1 on their respective axes show stronger membership and are more typical of their call cluster.

in the connected call clusters (Figure 2; Supplementary Materials, Tables S5 and S6). For example, *cluck* calls share secondary membership only with *check* calls (Figure 1(H); Supplementary Materials, Table S5). Yet, secondary membership values tended to be small in comparison to primary membership values (Table 2; Supplementary Materials, Table S5), indicating that the acoustic properties of *cluck* calls were relatively dissimilar to those of the *check* calls. By contrast, *zeer* and *se-er* calls, as well as *seee* and *ti-er* calls, showed strong relationships, as individual calls clustered towards the centres of their respective plots illustrating that first and second membership values were similar and that these call clusters were more alike than they were dissimilar (Figure 2(B,D), Table 2; Supplementary Materials, Table S5).

Primary and secondary memberships were not always reciprocal (Table 2; Supplementary Materials, Tables S5 and S6). For example, many *check* calls had secondary membership values with *zeer* ($n = 402$) and *se-er* ($n = 53$) calls (Figure 2(E,G)), whereas one or no calls in these call clusters, respectively, shared secondary membership with *checks* (Supplementary Materials, Table S5). Note that for *se-er/seee* and *check/seee* pairs, few calls had membership values with the secondary cluster (six and seven individual calls, respectively) and both primary and secondary membership values were low, indicating these calls fit poorly in both call clusters (Figure 2(C,F)).

Classifying call types on the continuum from discrete to graded structures

Typicality coefficients (TC) are measures of discreteness versus gradedness of individual calls, with values closer to 1 indicating that calls are more discrete. The typicality threshold, calculated using half the deviation from mean TC values and based on the corpus structure itself, defines the cut-off range for calls to be classified as graded, intermediate or discrete. The calculated threshold for typicality for the acoustic features dataset ranged from 0.21 to 0.43. Individual calls with TC values below the lower threshold (0.21) were considered graded; those with values greater than the higher threshold (0.43) were considered discrete, and those with values between the two were considered intermediate in gradation. Calls in the *cluck* cluster were discrete and had the highest mean TC values, followed by *checks. Ti-er* calls were designated as intermediate, with mean TC for the cluster (0.223) only slightly above the gradedness threshold (0.21), with *zeer, seee* and *se-er* (henceforth, we refer to the latter four call*s* as the '*seers*') yielding the lowest values overall, reflecting their graded designation (Table 3, Figure 3). Moreover, the distribution of calls in *cluck* cluster skewed right towards discreteness, whereas the distribution of calls in the remaining clusters skewed left towards gradedness (Figure 3).

Cluster assignment for the full breeding season dataset

Based on the fuzzy cluster results, the acoustic features of calls within each cluster (Table 1) and audio-visual inspection of the calls, we returned to the full breeding season dataset to assign all calls ($n = 13{,}485$) to one of the six clusters. A total of 7,642 calls (56.7%) were classified as *check*, 3,756 calls (27.9%) as *cluck*, 686 (5.1%) as *seee*, 548 (4.1%) as *se-er*, 444 (3.3%) as *ti-er* and 402 (3.0%) as *zeer*. Together, the *seers* accounted

Table 3. Mean, minimum and maximum, typicality coefficients (TC) by call cluster. Calls with TC values below 0.21 were designated as graded and those above 0.43 as discrete. Calls with TC values that fell between the two threshold values were designated as intermediate in gradedness.

Cluster	n	Mean	Minimum	Maximum	Designation
Check	598	0.355	0.0001	0.693	Intermediate
Cluck	277	0.706	0.0154	0.960	Discrete
Zeer	216	0.067	0.0012	0.197	Graded
Seee	128	0.100	0.0004	0.333	Graded
Se-er	184	0.156	0.0001	0.487	Graded
Ti-er	118	0.223	0.0001	0.699	Intermediate

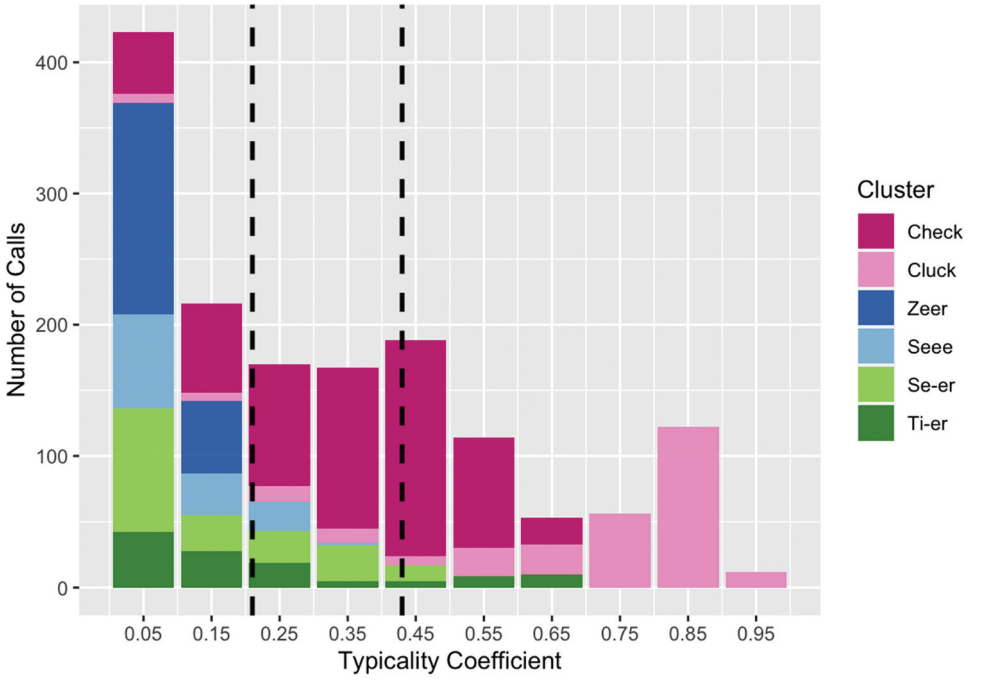

Figure 3. Histogram of typicality coefficients (TC) for individual calls used in acoustic analysis and their assigned cluster ($n = 1{,}521$). Each column shows the number of calls with a given TC, with different colours representing each call cluster. Thus, most calls across call clusters have low TC and only *cluck* calls show very high TCs. Dashed lines represent the typicality threshold (0.21–0.43), above which calls are considered discrete, below which they are considered graded and between which they are considered intermediate in structure.

for 15.5% of calls in the full breeding season dataset. A relatively small percentage of males gave all six call types (6.8% of 74 males), with increasing percentages of males giving five (9.5%), four (12.2%) and three (16.2%) call types. Most males produced two or one of the calls described (27.0% and 28.4%, respectively). We detected more call types per male with an increasing number of calls recorded, up to approximately 1000 calls when the line plateaued at six call types (Supplementary Materials, Figure S2).

Discussion

Male Red-winged Blackbirds exhibit a large and complex alarm call repertoire, with estimates ranging from 5 to 20 call types across alarm and social contexts (Orians and Christman 1968; Beletsky et al. 1986; Knight and Temple 1988; Beletsky 1991). Although for some time it has been noted that some male blackbird calls grade into each other, quantifying the extent of call gradedness has proven challenging (Orians and Christman 1968). Here, we used fuzzy clustering, a type of unsupervised clustering, on acoustic features measured from call spectrograms to organise vocalisations into clusters and to describe variation within and gradedness between call clusters (Hammerschmidt and Fischer 1998; Wadewitz et al. 2015; Fischer et al. 2017; Cusano et al. 2021), resulting in an acoustically sensitive and more objective classification of call types. Based on 1,521 high-

quality (high signal-to-noise ratio) calls recorded from 46 male blackbirds, fuzzy clustering identified six acoustically distinct alarm call clusters (Figure 1). The number of call clusters was remarkably similar to the number of call types identified visually or aurally in previous work and highlights the abilities of researchers to detect meaningful call similarities and differences. Our study, however, contributes new insights into the alarm call repertoire of this iconic species: fuzzy clustering more objectively classified the repertoire into call types, classified calls as discrete, intermediate or graded, and quantified the gradedness between them.

Soft clustering approaches have been applied to several mammalian taxa, yet despite their highly vocal nature, only two recent studies on birds have adopted this approach (captive Rooks (*Corvus frugilegus*) (Martin et al. 2024); Adelaide's Warbler (*Setophaga adelaide*) (Huang 2023)). Fuzzy clustering holds promise for new insights into the vocal repertoires of wild birds, particularly for species that produce acoustically graded alarm vocalisations (e.g. this study) and variable song types (e.g. Kaluthota et al. 2019). In the early adoption of fuzzy clustering to bird vocalisations, studies may be particularly helpful when applied to species, such as Red-winged Blackbirds, with well-described call repertoires. Male blackbirds produce acoustically variable calls, ranging from noisy and broadband to high-frequency and tonal (Table 1), and we compared call clusters identified by fuzzy clustering with published accounts and spectrograms of male blackbird calls (Orians and Christman 1968; Beletsky et al. 1986). Some call clusters identified by fuzzy clustering closely matched call types described in the literature, yet fuzzy clustering also grouped calls that had been previously split into different call types and also subdivided into multiple call types previously grouped into a single category (Table 4). Specifically, fuzzy clustering placed *check* calls, the most common call type in our recordings, within a single, large cluster ($n = 598$ calls) and classified them as intermediate in structure between graded and discrete (Figure 3, Table 3). These *check* calls had been split into four to five discrete call types in the literature (Orians and Christman 1968; Table 4; Beletsky et al. 1986), reflecting both the extensive variation in their acoustic structure and the challenge of classifying them by ear and hard clustering methods. Similarly, three types of *cluck*-like calls have been described (*chuck*, *cut* and *kwup*; Orians and Christman 1968; Table 4; Beletsky et al. 1986), whereas fuzzy clustering identified similar calls in our recordings as a single discrete call type with high

Table 4. A comparison of Red-winged Blackbird alarm calls identified in this study using fuzzy k-means clustering with qualitatively identified alarm calls from earlier studies (Orians and Christman 1968; Beletsky et al. 1986). We categorised calls described in earlier studies based on fuzzy clustering results; using spectrograms, we assigned calls to the cluster they were most similar. N/As indicate calls that did not match those identified in previous research.

	Previous studies	
This study	Beletsky et al. (1986)	Orians & Christman (1968)
Check	Check, Chonk, Chick, Peet, Chink	Check, Chick, Peet, Cheet
Cluck	Chuck	Chuck, Cut, Kwup
Zeer	Cheer	Cheer
Seee	N/A	Cheer
Se-er	Cheer	Cheer
Ti-er	N/A	Cheer

membership values ($n = 277$ calls, Figure 3, Table 3). On the other hand, earlier studies named only one type of *cheer* while noting extensive variation in call structure and our analysis identified three clusters of *cheer*-like vocalisations that were structurally graded (Table 1; the *seers*: *zeer*, $n = 216$, *seee*, $n = 128$, and *se-er*, $n = 184$) and one cluster that was intermediate (*ti-er*, $n = 118$). In the end, fuzzy clustering did not reveal novel calls but rather reorganised previously described calls in new ways based on similarities in their acoustic features and quantified gradation between call clusters.

Across taxa, discrete and graded call types often differ in production and function across behavioural contexts. Contact calls typically exhibit discrete structures and are described as short, soft calls used primarily to maintain contact with nearby conspecifics (Marler 2004). *Cluck* calls, identified by fuzzy clustering as the most discrete call within the repertoire of male blackbirds, were often used while foraging on the ground near their mates (K. A. Ray, personal obs.). Conversely, alarm calls for aerial predators tend to be high-pitched, pure-toned and not very localisable, which reduces predation risk to the signaller (Marler 1957). Male blackbirds produced four tonal, high-pitched *seers*, considered by others as *cheer* calls (Table 4). One of the *seer* calls, *seee*, may be equivalent to the 'hawk alarm call', a high-pitched variety of the *cheer* call given when raptors flew overhead (Nero 1956b; Orians and Christman 1968; Beletsky 1991). Blackbirds may also produce these high-pitched hawk alarm calls in contexts other than encounters with raptors (Beletsky 1991), which could explain the extent of variation and gradation in this call (Tables 1 and 3; Figures 1 and 2; Supplemental Materials, Table S5). In blackbirds, the graded and tonal calls (the *seers*) may be associated with escalating alarm contexts, as in ground squirrels that exhibit urgency-based alarm systems (McRae 2020). Additional research on the function of call clusters identified by fuzzy clustering is needed to further explore whether structural variations reflect functional specialisation in blackbirds.

Graded alarm signals often reveal the increasing urgency of response required by receivers to minimise predation risk (McRae 2020). In mammals and birds, urgency-based alarm call systems communicate the relative perception of a threat and predation risk (e.g. size, speed or predator type, i.e. aerial vs. terrestrial). Signallers vary call rate, number of call elements, call structure or a combination of these properties and may also combine calls to reveal different aspects of predator identity and predation risk (Templeton et al. 2005; Suzuki 2014). In Superb Fairy-wrens (*Malurus cyaneus*), the higher overall maximum frequency of aerial alarm calls combined with an increased number of call elements denotes the most threatening encounters for fairy-wrens (Fallow and Magrath 2010). The use of graded alarm calls by male blackbirds parallels these call systems, but with the added complexity that blackbirds have multiple call types that may communicate response urgency. The *seers* (*zeer, seee, se-er* and *ti-er*) exhibited extensive overlap in acoustic features, revealing a gradual shift in acoustic structure rather than clear separation of calls (Figures 1 and 2, Table 1). As such, the gradation within the *seer* calls may reflect increased response urgency by receivers during threatening encounters. Past studies described an urgency-based increase in call rate in response to moving predators (Beletsky 1991) and blackbirds may additionally use the extensive structural variations in their graded calls to communicate information about other levels of threat, such as predator size or proximity. Blackbirds also switch calls upon detection of disturbance (Beletsky et al. 1986) and these graded signals may be used in specific orders to communicate levels

of risk. While it remains unclear under what contexts blackbirds use graded calls identified in this study, model presentation and playback studies would uncover whether varying levels of risk are encoded in these complex alarm calls.

Thus far, fuzzy clustering has been used to describe vocal repertoires at the level of species, but with a robust sampling design, individual repertoires could be investigated as well. With the caveat that we did not sample most males heavily enough to ensure complete sampling of their call repertoire, we found that relatively few males gave all call types in our full breeding season dataset (Supplemental Materials, Figure S2). Most calls recorded were *check* calls, with other call types less well represented among calls in recordings. In a nest defence context, Knight and Temple (1988) report a similar pattern with few males producing all five call types they observed. As the number of calls recorded per male increased, so did the number of call types, up to about 1000 recorded calls after which point six call types were consistently detected (Supplemental Materials, Figure S2). Future study of individual complex call repertoires, as well as application of this approach for song note repertoires, will require intense sampling of individuals.

The structure of vocalisations, including calls, may vary geographically, thereby reflecting patterns of divergence across populations (e.g. Laiolo et al. 2001; Luttrell and Lohr 2018; Lengagne et al. 2020). Differences in call structure among populations may be attributed to genetic distance (Laiolo et al. 2001) and large-scale habitat differences among ecosystems (Lengagne et al. 2020). The male blackbirds in our Michigan study populations produced call types similar to ones noted in studies of this species in Washington and California (Table 4). However, geographic variation seems to exist as some of the calls present in the Michigan population were described in some, but not all other studied populations (Table 4, e.g. *seee* and *ti-er*). These differences in call production could reflect meaningful population differences, possibly due to geographic distances and accompanying genetic distances among populations among study sites (WA, CA v. MI). Divergence in alarm call production among populations of blackbirds could be differentially selected, given the direct influence of alarm calls on survival and reproductive success.

Although fuzzy clustering is well suited to describing graded vocal repertoires (Wadewitz et al. 2015; Cusano et al. 2021), cluster solutions remain dependent on the data used to generate them. Here, our six-cluster solution was built on the 1,521 calls included in the acoustic features dataset; however, a different sample of calls could yield slightly different cluster solutions. For example, *growls* are given by males in aggressive contexts (Nero 1956a; Knight and Temple 1988), but few males in our study gave them. We did not include *growls* in our analysis simply because they were not produced in sufficient sample size to capture natural variation within the calls. The addition of these rare calls in the fuzzy analyses of the blackbird system could alter the 'gradedness' categories defined by the typicality thresholds, as well as the clusters themselves. Nevertheless, a major advantage of fuzzy clustering is that we can examine the degrees of gradedness within the blackbird repertoire (Figures 2 and 3; Tables 2 and 3), which is not possible using hard-clustering techniques that force calls into a single cluster (Bezdek 1981). Moreover, fuzzy clustering is more objective, even though its iterative nature relies on somewhat subjective decisions to refine results and draw conclusions about cluster solutions. Thus, transparency in reporting the data distributions, analytic procedures, internal validation metrics and decision

making is important when running fuzzy analyses (Wadewitz et al. 2015), as doing so will allow for comparative studies of vocal repertoires of blackbirds and other highly vocal species.

In conclusion, fuzzy clustering revealed that the alarm call repertoire of adult male Red-winged Blackbirds contains six call type clusters that ranged from discrete to graded in acoustic structure. Further study is required to identify the specific contexts associated with this signal classification and to infer possible functional differences across call types. The use of graded signals in the blackbird alarm system has the potential to expand their communicative ability, possibly by providing additional levels of response urgency and meaning within calls than previously recognised. The six alarm calls described here are comparable to those reported in published qualitative studies, although overall our analysis identified fewer call types than past studies. Whether this is simply the result of differences in methods (qualitative vs. quantitative) or the product of divergence or other geographic-related differences requires additional testing. Regardless, our study provides the first quantitative categorisation of the alarm calls of male Red-winged Blackbirds, which is a key step in more fully understanding this species' acoustic communication system and in applying these methods to classify call repertoires across diverse taxa (Bradbury and Vehrencamp 2011). Finally, more clarity surrounding the variation within calls and associated behaviours may contribute to the rapidly expanding species monitoring efforts that rely solely on autonomous recordings of vocalisations in the absence of sightings (Oestreich et al. 2024). Fuzzy clustering allowed us to quantify gradedness between call clusters, illustrating the variation within and between call clusters and opening up new avenues for research in this well-studied species.

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Author contributions

CRediT: **Katelyn A. Ray:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing; **Katharine S. Maurer:** Data curation, Formal analysis, Investigation; **Dana A. Cusano:** Formal analysis, Methodology, Software, Writing – review & editing; **Mark E. Hauber:** Conceptualization, Funding acquisition, Writing – review & editing; **Sharon A. Gill:** Conceptualization, Funding acquisition, Methodology, Project administration, Software, Supervision, Visualization, Writing – original draft, Writing – review & editing.

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Data availability statement

The data that support the findings of this study are available from the corresponding author, [K.A. R], upon reasonable request.

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