Who's Your Neighbor? Acoustic Cues to Individual Identity in Red Squirrel (Tamiasciurus Hudsonicus) Rattle Calls

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Who's your neighbour? Acoustic cues to individual identity in red squirrel (*Tamiasciurus hudsonicus)* rattle calls.

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Abstract North American red squirrels (*Tamiasciurus hudsonicus*) often produce a loud territorial rattle call when conspecifics enter or invade a territory. Previous playback experiments suggest that the territorial rattle call may indicate an invader's identity as squirrels responded more intensely to calls played from strangers than to calls played from neighbors. This dear-enemy effect is well known in a variety of bird and mammal species and functions to reduce aggressive interactions between known neighbours. However, although previous experiments on red squirrels suggest some form of individual differentiation and thus recognition, detailed acoustic analysis of potential acoustic cues in rattle calls have not been conducted. If calls function to aid in conspecific identification in order to mitigate aggressive territorial interactions, we would expect that individual recognition cues would be acoustically represented.

Our work provides a detailed analysis of acoustic cues to identity within rattle calls. A total of 225 calls across 32 individual squirrels from Sheep River Provincial Park, Kananaskis, AB, Canada, were analyzed with discriminant function analysis for potential acoustic cues to individual identity. Initial analysis of all individuals revealed a reliable acoustic differentiation across individuals. A more detailed analysis of clusters of neighbouring squirrels was performed and results again indicated a statistically significant likelihood that calls were assigned correctly to specific squirrels (55-75% correctly assigned); in other words squirrels have distinct voices that should allow for individual identification and discrimination by conspecifics.

Keywords: vocal communication, territory calls, red squirrel, dear-enemy, individual identity

After establishing territorial relationships, often through protracted aggressive interactions, individuals in many territorial species subsequently respond less aggressively to intrusions by neighbours than to intrusions by strangers, a phenomenon that has been termed the dear-enemy effect (Fisher, 1954; Ydenberg et al., 1988). The first hypothesis of this effect, that of familiarity, suggests that once a relationship has been established, individuals become familiar with each other (Temeles, 1994). This resulting familiarity affords territory holders fewer overall aggressive interactions with known neighbours and therefore reduces energy costs and risk of injury (Wilson, 1975).

A second component underlying the dear-enemy effect is captured under the threat level hypothesis. Here, Temeles (1994) suggests that neighbours and strangers may compete for resources at different levels and therefore may represent different levels of threat to the territory holder. In other words, strangers may be looking for a new territory and thus represent a greater threat than neighbours who may be looking for food and mates (Ydenberg et al., 1988; Temeles, 1994). Additionally, the threat-level hypothesis aids in describing situations in which neighbours represent a greater threat than strangers to a territory holder (Temeles, 1994). In some cases particular neighbours may be untrustworthy and represent a greater threat than strangers, thus requiring a more aggressive interaction (Olendorf et al., 2004; Muller and Manser, 2012). For example, in red-winged blackbirds (*Agelaius phoeniceus*), males alter interactions with neighbouring males who were more successful at extra-pair copulations (EPC) (Olendorf et al., 2004). Males will use body size cues as well as behaviours like territory boundary intrusion to assess a neighbouring male's EPC success. Playback and simulated intrusion experiments have revealed that males increase aggression to towards those neighbours who are deemed cheaters of the dear-enemy relationship by intruding on territory boundaries (Olendorf et al., 2004).

In many cases, the dear-enemy effect appears to hinge on individually distinctive vocalizations that allow for vocal recognition of neighbours (and discrimination of strangers) at a distance. Individually distinctive territorial vocalizations and the dear-enemy effect have been well documented in many bird species (for review see Stoddard, 1996). For example, individual Carolina wrens (*Thryothorus ludoviciaus*) can reliably discriminate the territory advertisement calls of neighbours from those of strangers. Playback experiments also indicate that individual discrimination of these calls results in reduced aggressive responses to the calls of neighbours compared to those of strangers (Hyman, 2005). In some bird species there are dialect level differences that individuals may use for identification. For example, in skylarks (*Alauda arvensis*) neighbouring males share particular sequences of syllables within their songs (Briefer et al., 2011). In contrast males that have settled into different areas, in other words strangers, have almost no syllable sequences in common. Playback experiments revealed that these acoustic signals also resulted in a dear-enemy effect, as there was reduced aggression towards neighbours when compared to strangers (Briefer et al., 2011).

The dear-enemy effect has been explored predominantly in reptiles, amphibians and territorial bird species. However, some mammal species are also more tolerant of neighbours than strangers. For example, male deer mice (*Peromyscus maniculatus*) fight significantly less with familiar male neighbours than with new or unfamiliar neighbours (Healy, 1967). Banner-tailed kangaroo rats (*Dipodomys spectabilis*) also tend to tolerate territorial neighbours more than strangers. Neighbour pairs were observed to interact more peaceably than were stranger pairs in both playback and arena experiments (Randall, 1984; 1989), as Hare (1998) reported for arena interactions among juvenile Richardson's ground squirrels (*Urocitellus richardsonii*). American pika (*Ochotona princeps*) also produce short territorial calls when leaving their territories (Conner, 1985). These calls are thought to announce the presence of an individual pika on a neighbouring territory and thus reduce the number of aggressive encounters. Experiments indicated that territorial intrusions, and resulting aggression, were reduced when calls were played from empty territories as compared to silence in empty territories (Conner, 1985).

Research conducted on neighbour interactions in red squirrels (*Tamiasciurus hudsonicus*) indicates that individuals produce more intense responses to playback of the species-specific territorial rattle call when produced by strangers than when produced by familiar neighbours. This pattern of reduced aggressive response to calls of established neighbours suggests that there may be benefits to solitary squirrels that tolerate and maintain relationships with current neighbours (Price et al., 1990). Specifically, such tolerance in the context of an established territorial relationship may be less costly than re-establishing territorial relationships with new neighbours (Temeles, 1994).

In fact, trespassing and cone pilfering is ubiquitous in western red squirrels and represents a major threat to survival (Rusch and Reeder, 1978; Price et al., 1990; Donald and Boutin, 2011). Cone losses to theft by neighbours can account for up to 84% of the stored food supply that individuals rely on to get through long, harsh winters in the temperate zone (Gerhardt, 2005). Given the energetic constraints facing these small-bodied, non-hibernating mammals overwintering in boreal forests, cone loss may represent as serious a threat to red squirrel survival as do many forms of predation. If so, it would benefit territory holders to be able to recognize and differentiate conspecific neighbours from strangers.

Although previous research in red squirrels suggested that individuals distinguished between neighbours and strangers (Price et al., 1990), it was not clear if this was due to acoustic cues within the territorial rattle call or if territory holders were using other visual or olfactory cues. Our research begins with a detailed acoustic analysis of individual rattle calls in order to explore and examine any potential cues to an individual's identity. Future detailed playback experiments will be conducted in order to explore responses to current neighbour compared to floating stranger rattle calls.

1. Methods

1.1 Study site and subjects

Research was conducted at the R.B. Miller Field Station in the Sheep River Valley of Kananaskis Provincial Park, Alberta, Canada (50°39′ N, 114°39′ W), which is situated in the foothills of the Canadian Rockies. The habitat in the Sheep River Valley is a mix of aspen (*Populus tremuloides)* parkland and montane (sub-alpine) coniferous forest composed primarily of lodgepole pine (*Pinus contorta*) and white-spruce (*Picea glauca*). Red squirrels are more common in the latter forest types in North America where they hoard and feed on the seeds of conifers (Smith, 1968; Gurnell, 1984). Research on territorial vocalizations focused on 32 individuals from a marked population of 47. Each of these 47 squirrels maintained an exclusive territory (approximately 0.5 – 1.0 ha) containing at least one central midden with a supply of stored cones, which was actively defended against intruders. Within this population individual squirrels were found in clusters of territories that were formed due to uninhabitable natural divisions in the environment. These divisions included; large stands of aspen, ponds or large portions of standing water, and human or animal created pathways.

Research was conducted in three consecutive years (2005-2007) between May and October. During this period the population remained quite stable. However, there were five changes in the territory cluster structure. In territories NW12 (2007) and NW14 (2006) the owners disappeared during the winter months and were subsequently replaced by new individuals the following spring. Additionally, in territories NW2, NW8 and NW17 the females inhabiting these areas allowed an offspring to remain and take up a portion of the territory. This bequeathal is not an unusual practice and has been observed in other populations of red squirrels (Berteaux and Boutin, 2000).

Data collection focused on individual squirrels, their vocalizations and the behaviours associated with those vocalizations. Each individual squirrel was randomly selected and followed for a period of 15 minutes during which time scan samples were taken every two and half minutes to record the behavioural occurrence and all vocalizations produced. If conspecifics were encountered, we noted who was involved in the disturbance and details of the squirrel's response, while a continuous recording was made of the vocalizations produced. During recordings individual squirrels were between 5-10 meters from the recording equipment. Vocalizations were recorded using a digital Marantz PMD660 recorder and a Sennheiser ME66 shotgun microphone with a K6 powering module and a Sennheiser MZH60-1 windscreen. All vocalizations were digitally recorded at 44.1 kHz with 16-bit accuracy.

In order to facilitate individual identification within and across field seasons, each squirrel was captured in its territory using a live-trap baited with peanut butter (Tomahawk Live Trap Company, Tomahawk, WI, USA), and unique dye marks (Clairol #52 Black) and ear tags were applied (Tag#1005-1; National Band and Tag Company, Newport, KY, USA). Trapping and handling techniques, and other research protocols, were approved by the Animal Research Ethics Board at Grant MacEwan University (01-09-10-R1), the Animal Welfare Committee of the University of Lethbridge (08-09) and by Alberta Sustainable Resource Development, Fish and Wildlife Division (Research Permit GP 49514; Collection License CN 49535). Details on the capture, trapping and marking protocol can be found in Digweed and Rendall (2009).

1.2 Vocal sample and measurement

Red squirrels are known to produce loud 'rattle' calls when moving through their territories and in some cases when encountering conspecific intruders. In order to explore any potential acoustic cues to identity that conspecifics may use in recognizing neighbours, we first limited the collected vocal recordings to those individuals who had been identified and produced territorial rattle calls while in their own territory.

To standardize the dataset and reduce potential confounding influences, we attempted to construct a fully balanced sample including only individuals who had produced at least three rattle calls across the years 2005-2007. We felt that all years could be included in our sample due to the stability in territory owners and the relative infrequency of turnovers that would have resulted in new individuals in the overall population and territory clusters From this sample, we then selected only the best quality sounds for acoustic analyses. In the end, the sample for analysis included 32 different individuals, who contributed a total of 225 different rattle calls.

1.3 Acoustic analysis

To examine potential structural differences between individual rattle calls, we measured a large number of specific acoustic features designed to comprehensively characterize the temporal, intensity and spectral characteristics of each call type. All measurements were conducted using PRAAT© 5.1 (Boersma, 2001). For all rattle calls we measured the overall call duration as well as note duration within the rattle. Each rattle call is comprised of a series of notes that are produced in a long sequence that can vary in duration (Fig. 1). Because there may be differences in the duration of these notes that may be salient to listeners, we felt it was important to quantify the temporal features of the notes. We did this by randomly selecting five notes from within each rattle and taking the average duration of those notes.

We also characterized the abruptness of call onset, which translates perceptually as its 'plosiveness'. We used four measures of call plosiveness by using the intensity object supplied by PRAAT©. An intensity object represents an intensity contour algorithm at linearly spaced time points with values expressed in dB (amplitude) The intensity at every time point is a weighted average over many neighbouring time points (Boersma, 2001). We used this intensity contour to measure very specific points in each call; the start intensity of the overall call (reported in dB), the peak intensity of the overall call (reported in dB) and the time from call onset to maximum intensity expressed both as an absolute time (ms) and as a proportion of total call duration (%).

We also measured several spectral features of rattle calls. Although these calls typically had a noisy, broadband structure, there was a stable fundamental frequency (F_0), which determines the sounds perceived pitch, and additional levels of spectral energy apparent. Therefore, we used the first four formants, or peaks in spectral energy, to capture the distribution of energy within the call. Here, we used auto-correlation based Linear Predictive Coding (LPC) to identify the spectral peaks. LPC routinely identifies spectral peaks of energy that represent the resonances of the vocal tract (Owren and Bernacki, 1997). Spectral measures were taken from a spectral slice centered on the midpoint of the rattle using a 250-point Fast Fourier Transform and retained as a frequency (Hz) measure.

1.4 Statistical analysis

We used multivariate discriminant function analysis (DFA) to evaluate potential acoustic differences within rattle calls as produced by the different individuals. DFA highlights the variables contributing to discrimination among groups (in this case individuals) and quantifies how accurately they allow groups to be discriminated (Tabachnick and Fidell, 2007).

The degree of discrimination among groups in DFA is typically assessed in two ways. First, the statistical significance of a given degree of discrimination is assessed using an overall test statistic, Wilks' Lambda. This test statistic varies from 0 – 1, where zero indicates perfect discrimination among groups and 1 indicates no discrimination among groups. The significance of the test statistic can be evaluated using an *F*-ratio or *Chi-square* transformation of the Wilks' Lambda value (Klecka, 1980).

An additional and more practical metric for assessing the degree of discrimination among groups is provided by the relative success of the discriminant functions in classifying cases into their appropriate groups. Here, the degree of successful classification is typically evaluated according to how much it exceeds chance classification and this can provide a more practical sense of the degree of differentiation among groups. In this case, it will provide a more ecologically relevant sense of how well rattles can be reliably assigned to each individual squirrel.

2. Results

Two DFA analyses were conducted on the 225 rattle calls. The first analysis attempted to classify the rattles, across all of the acoustic variables measured, with each of the 32 different individual squirrels. The DFA yielded an overall Wilks' Lambda of 0.058. This value was associated with a statistically significant degree of variation in rattles across the 32 individual squirrels ($F=1.9$, $P<0.05$). The variables that contributed the most to the classification were the average note duration ($F=4.6$, $P<0.05$), formant frequency two ($F=3.4$, $P<0.05$), and formant frequency four ($F=2.6$, $P<0.05$). Because the Wilks' Lambda statistic was close to the theorized lower limit of zero for this test statistic, there was good discrimination between the groups and thus differentiation in rattle calls among individuals appears to be reliable.

Reliable differentiation among groups was also evidenced in more practical terms by the results of discriminant analysis classification of calls. DFA successfully classified 31% of the calls to the correct individual.. Although the accuracy seems relatively low at 31%, the Wilks' Lambda score was well below one and successful classification of calls by chance alone would have been only 6.75% for this sample of 32 individuals. Thus the observed level of classification success represents a marked improvement over chance.

We also ran a second DFA analysis on the dataset with a slightly different organization reflecting the spatial organization of individuals within the overall population. Because all 32 individual squirrels did not live in close proximity to each other, it seems natural that some acoustic distinction may exist within particular neighborhoods or what we termed territory clusters. In other words, rattle call acoustic variation among individuals may be more reliably classified within the cluster of territories in which a squirrel naturally lives. Therefore, we grouped our 32 individuals into the territory clusters in which they occurred. These clusters included the following territories; a) NW 2 -8 (nine individuals, 67 calls), b) NW 14 - 21 (eight individuals, 53 calls), c) NW 24 – 36 (nine individuals, 68 calls), and d) SW 2 –17 (six individuals, 37 calls).

In this analysis DFA yielded overall Wilks' Lambda and test statistic scores of; a) 0.091 (F=1.8, P<0.05), b) 0.017 (F=3.1, P<0.05), c) 0.057 (F=2.3, P<0.05), d) 0.024 (F=2.8, P<0.05). The variables that contributed to the classification included; a) average note duration (F=5.0, P<0.05), formant frequency two (F=3.5, P<0.05), and fundamental frequency (F=2.0, P<0.05), b) formant frequency four (F=4.7, P<0.05), formant frequency three (F=4.3, P<0.05), and average note duration (F=3.6, P<0.05), c) formant frequency two (F=3.8, P<0.05), fundamental frequency (F=3.5, P<0.05), and average note duration (F=2.6, P<0.05), d) formant frequency four (F=7.2, P<0.05), formant frequency two (F=6.4, P<0.05), and formant frequency three

(F=4.0, P<0.05). Once again the Wilks' Lambda scores, in each territory cluster, were close to the theorized lower limit of zero for this test statistic, which indicates good discrimination between groups. Hence, the degree of differentiation in rattle calls among individuals within each of their territory clusters also appears to be reliable.

Additionally, DFA successfully classified a) 55%, a 6.6% improvement over chance, b) 66%, a 7.7% improvement over chance, c) 74%, an 8.4% improvement over chance, and d) 75%, a 7.4% improvement over chance, of calls within each territory cluster (Table 1). The average across all clusters was 67%, which is an improvement on the original classification across all individuals of 31% Finally, in order to confirm that the improvement in classification in the smaller territory clusters was not due to a smaller sample size, we ran several DFA analyses in which individual placement was randomly generated. These resulted in an average classification success of 25.3% with high Wilks' Lambda scores (range of 0.51 – 0.66) and non-significant p-values (range of P = 0.18 – 0.93). Therefore, because of the improvement in classification from both the original DFA and the DFA based on randomly associated individuals, we feel that the grouping of individual squirrels into their associated neighbourhoods better represents the actual recognition task that each squirrel would be faced with.

3. Discussion

Red squirrel rattle calls appear to have reliable acoustic characteristics that would allow individuals to recognize each other. Discriminant analyses revealed that overall 31% of rattles were correctly assigned to the individual that produced them. Although this classification is relatively low it is 4.6 times above chance classification (6.75%). Moreover, when individual squirrels were clustered into the neighbourhoods of territories in which they live, classification success was markedly improved. We felt that these territory clusters more accurately represented the neighbours that each squirrel would interact with and have to recognize. The average classification of the territory clusters was 67% with each cluster having individual classifications of 55%, 66%, 74% and 75%. Again, these are marked improvements from chance for each cluster of 6.6%, 7.7%, 8.4% and 7.4%, which on average represent an increase in accuracy of nine times with the inclusion of the acoustic variables measured.

Varying levels of discriminant classification accuracy are accepted as evidence for individual identity in vocalizations. Much of individual identity work has focused on social contact calls in the primate literature. For example, classification of rhesus monkey contact calls at 79.4% was an improvement on the 6% chance classification of 17 individuals (Rendall et al., 1998). Conversely, in spider monkeys call classification appears low at 50% across 14 individuals. However, chance was 7.1% and therefore by including the acoustic cues classification was improved by seven times (Chapman and Weary, 1990). We therefore feel that both of our analyses reveal reliable acoustic cues to individual identity that squirrels should attend to.

Individual recognition may result in survival benefits for squirrels that are associated with the dear-enemy effect (reviewed by Ydenberg et al., 1988; Temeles, 1994). As stated earlier, several species display reduced aggression toward familiar neighbours that are seemingly less of a threat to territory holders. In red squirrels many of the territorial interactions are regarding food stores (Smith, 1981; Price et al., 1990; Donald and Boutin, 2011; Digweed personal obs.). Individuals will often make 10 or more trips a day through several territories searching for food and may steal some or a substantial portion of a territory owner's cache (Digweed personal obs.; Gerdhardt, 2005). Thus it is likely for a territory owner to encounter neighbours during daily foraging activities. The ability to recognize individuals via rattles may allow for reduced aggression in interactions with known neighbours and for the recognition of strangers who may attempt to usurp control of the territory.

Moreover, the identification of conspecifics would allow squirrels to adjust the level of aggressive interaction required with neighbours who represent more of a threat than others. For example, age and food availability have been found to alter the rate that a squirrel pilfers. Removal experiments indicated that younger squirrels with smaller cone caches were more likely to pilfer from neighbours (Donald and Boutin, 2012). Thus, different neighbours may represent a different level of threat to a territory holder. This idea is consistent with the threat-level hypothesis, which suggests that a neighbour may invade for food or mates whereas a stranger may invade to take over the territory, therefore representing different levels of threat (Temeles, 1994). Northern harriers (*Circus cyaneus*) exemplify such threat-based differentiation among conspecifics in responding more aggressively to neighbours than to floating strangers because neighbours spend more time flying over boundaries and are more likely pilfer food items and expand their territory than are strangers (Temeles, 1990). Thus, it seems reasonable that red squirrels would use rattles to recognize different neighbours as well as discriminating neighbours from strangers and adjusting the level of aggression accordingly.

Our acoustic analysis provides further evidence for the dear-enemy phenomenon, be it a product of mechanisms predicted by the threat-level or familiarity hypothesis, in red squirrels. Future research will involve playback experiments that will document territory holder responses to neighbour- as compared to stranger-produced rattle calls. These playbacks will serve as the critical test for acoustic recognition of individuals and any resulting dear-enemy effect. Additionally, these experiments will address whether responses of signal recipients are modulated according to the relative threat posed by different individual neighbours, and thereby differentiate between dear-enemy effects attributable to mechanisms predicted under the familiarity and threat-level hypotheses.

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Table 1. Individual acoustic differences of red squirrel rattle calls within each of four different territory clusters: results of discriminant function classification.

Territory Clusters of Neighbours*	**Correct Individual Membership within Cluster Percent/Count**	**Incorrect Individual Membership within Cluster Percent/Count**	**Total Percent/Count**
NW 2 – 8	55 (37)	45 (30)	100 (67)
NW 14 - 21	66 (35)	34 (18)	100 (53)
NW 24 - 36	74 (50)	26 (18)	100 (68)
SW 2 - 17	75 (27)	25 (10)	100 (37)
Average	**67**	**33**	**100**

*Wilks' Lambda scores of 0.091 (F=1.8; P<0.05); 0.017 (F=3.1; P<0.05); 0.057 (F=2.3; P<0.05); 0.024 (F=2.8; P<0.05) respectively.

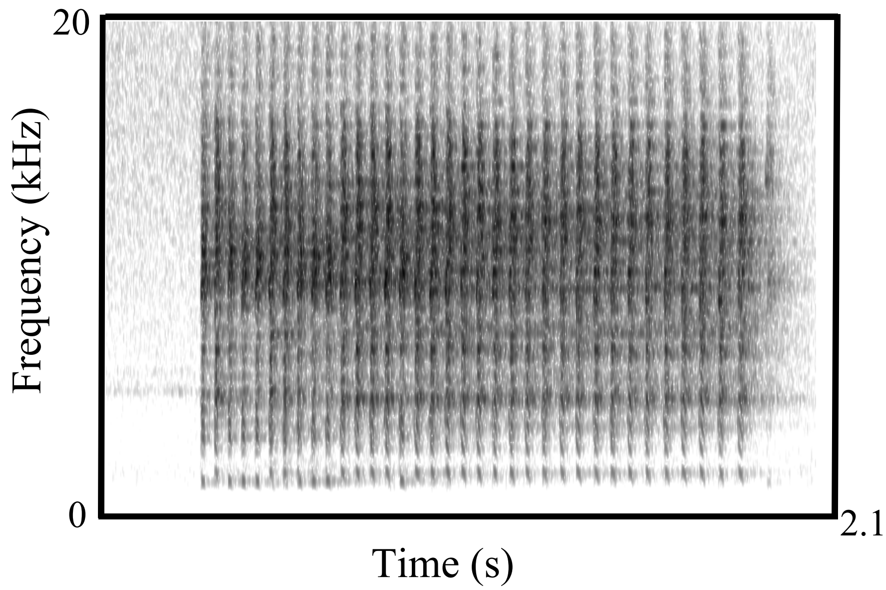

Fig. 1 Spectrogram of a rattle call. Spectrogram was produced in PRAAT 5.1 © using a Hanning window and overlapping 220-point fast-Fourier transforms with a 7.5ms time step and 44.3 Hz frequency step.