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RESEARCH ARTICLE

Differences in aggressive responses do not contribute to shifts in a sapsucker hybrid zone

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ABSTRACT

Interspecific interactions, such as aggressive territorial behaviors, can be important in establishing range boundaries, especially in hybrid zones where 2 divergent taxa meet and interbreed. Further, differences in the aggressive responses among hybridizing taxa can be important in moving hybrid zones, especially when there are strong asymmetries in their aggressive interactions. To determine how between-taxon interactions may be contributing to hybrid zone movement between 2 species of sapsucker, we studied an aspect of territory maintenance: aggression toward a territory intruder between species. Using a series of field experiments involving playback and taxidermic mounts, we tested whether Red-naped (*Sphyrapicus nuchalis*) and Red-breasted (*S. ruber*) sapsucker differ in their levels of aggressive behavior, thereby influencing the dynamic nature of the hybrid zone between these species. We found that 2 of the 3 aggressive response variables we measured differed between the 2 species. Red-naped Sapsuckers showed higher levels of aggression, as measured by overall acoustic aggression and the time it took a bird to reach its closest position to a taxidermic mount. These differences, however, were opposite of our prediction that Red-breasted Sapsuckers would show a greater aggressive response, thus contributing to the expansion of Red-breasted Sapsuckers and movement of the hybrid zone. Despite these overall differences between species, we found no significant differences between sapsuckers in sympatry. Further, we argue that acoustic aggression may not be a good proxy for physical aggression, and may instead represent a difference in communication methods between species. We suggest that species asymmetries in territorial aggressive responses do not cause hybrid zone movement in this system. Nevertheless, our work highlights the importance of comprehensive studies of hybrid zones in assessing the mechanisms that may be important in maintaining species boundaries between hybridizing taxa.

Keywords: aggression, hybrid zone, sapsucker, *Sphyrapicus*, movement

Las diferencias en las respuestas agresivas no contribuyen con los corrimientos en una zona hibrida de *Sphyrapicus*

RESUMEN

Las interacciones entre especies, como los comportamientos territoriales agresivos, pueden ser importantes para establecer límites de rangos, especialmente en las zonas híbridas donde dos taxa divergentes se encuentran y se entrecruzan. Más aún, las diferencias en las respuestas agresivas entre los taza que hibridan pueden ser importantes en determinar el corrimiento de las zonas híbridas, especialmente cuando hay fuertes asimetrías en sus interacciones agresivas. Para determinar cómo las interacciones entre taxa pueden estar contribuyendo al corrimiento de la zona híbrida entre dos especies de *Sphyrapicus*, estudiamos un aspecto del mantenimiento del territorio: la agresión entre especies hacia un intruso territorial. Usando una serie de experimentos de campo que incluyeron la reproducción de sonidos previamente grabados y montajes de taxidermia, evaluamos si *S. nuchalis* y *S. ruber* diferían en sus niveles de comportamiento agresivo, de este modo influyendo la naturaleza de la dinámica de la zona híbrida entre estas especies. Encontramos que dos de las tres variables de respuesta agresivas que medimos difirieron entre las dos especies. *S. nuchalis* mostró niveles más altos de agresión, medida como agresión acústica general, y el tiempo que le llevó a un ave alcanzar su posición más cercana a un montaje de taxidermia. Estas diferencias, sin embargo, fueron opuestas a nuestras predicción de que *S. ruber* mostraría una mayor respuestas agresiva, contribuyendo de este modo a la expansión de *S. ruber* y al corrimiento de la zona híbrida. A pesar de estas diferencias generales entre especies, no encontramos diferencias significativas entre las especies de *Sphyrapicus* viviendo en simpatría. Más aún, argumentamos que la agresión acústica podría no ser un buen indicador de la agresión física, y puede en cambio representar una diferencia en los métodos de comunicación entre las especies. Sugerimos que las asimetrías de las especies en sus respuestas territoriales agresivas no causan el corrimiento de la zona híbrida en este sistema. Sin embargo, nuestro trabajo subraya la importancia de estudios integrales de las zonas híbridas para evaluar los mecanismos que pueden ser importantes para mantener los límites entre especies que hibridan entre sí.

Palabras clave: agresión, corrimiento, *Sphyrapicus*, zona híbrida

INTRODUCTION

How species interact with each other can be extremely important for how they are distributed across the landscape (West-Eberhard 1983, Case et al. 2005, Price and Kirkpatrick 2009). Species interactions can also influence where range boundaries occur (Case et al. 2005) and contribute to shifts in the distributions of species (Pearson and Rohwer 2000, McDonald et al. 2001). Hybrid zones, where 2 divergent taxa meet and interbreed, are excellent systems in which to assess the role behavioral differences play in maintaining the ranges of overlapping, interbreeding taxa (Harrison 1993, Coyne and Orr 2004).

Interspecific behavioral interactions, and especially aggressive interactions, can play a key role in establishing range boundaries (West-Eberhard 1983, Case et al. 2005, Fadarimo et al. 2009, Price and Kirkpatrick 2009, Jankowski et al. 2010, Pasch et al. 2013). Aggressive interactions between species often act along with abiotic, environmental conditions to limit the ranges of species (Bronson et al. 2003, Price and Kirkpatrick 2009, Pasch et al. 2013, McQuillan and Rice 2015, Taylor et al. 2015). These behavioral, interspecific interactions can lead to parapatric range boundaries that are stable across both ecological and evolutionary time (Price and Kirkpatrick 2009). However, in the face of climate change, interspecific interactions can also contribute to distribution shifts, especially when there are strong differences in the aggressive behaviors between species at range boundaries (e.g., Bronson et al. 2003, Jankowski et al. 2010, Pasch et al. 2013, Taylor et al. 2015).

Asymmetries in aggressive behaviors between species at range boundaries can be especially important for understanding the dynamics of moving hybrid zones (Pearson and Rohwer 2000, Perry et al. 2001, Bronson et al. 2003, Buggs 2007, McQuillan and Rice 2015, While et al. 2015). In the Hermit/Townsend's warbler (*Setophaga occidentalis/S. townsendi*) hybrid zone, male Townsend's Warblers are "hyper-aggressive" toward male Hermit Warblers and displace them from territories; this behavior has, in part, contributed to rapid movement of the hybrid zone (Pearson and Rohwer 2000, Krosby and Rohwer 2009, 2010). In many systems (e.g., McDonald et al. 2001, Bronson et al. 2003, Stein and Uy 2006), female choice can act in concert with differences in inter-male interactions to influence hybrid zone dynamics. In a *Manacus* hybrid zone, for example, female choice for yellow coloration and the greater aggressive response of yellow-colored males toward white-colored males has led to the unidirectional movement of yellow plumage far ahead of the genetic contact zone (Brumfield et al. 2001, McDonald et al. 2001, Stein and Uy et al. 2006).

We investigated how aggressive behavior might influence hybrid zone structure and movement within a sapsucker (Aves: *Sphyrapicus*) hybrid zone. This is an excellent system in which to address these questions because males are highly territorial and will attack and chase intruders (Seneviratne et al. 2012, Walters et al. 2014a,b). Furthermore, previous work on a hybrid zone in British Columbia between Red-breasted (*Sphyrapicus ruber*) and Yellow-bellied (*S. varius*) sapsuckers suggested that the aggressive responses of individual sapsuckers can vary both within and between species (Seneviratne et al. 2012). We studied Red-breasted and Red-naped sapsuckers (*S. nuchalis*), which meet and hybridize along a narrow contact zone that stretches from northeastern California to southern British Columbia (Howell 1952, Johnson and Johnson 1985, Trombino 1998). In parts of the contact zone, there have been drastic shifts in the distributions of each species (Howell 1952, Johnson and Johnson 1985). Red-breasted Sapsuckers have expanded eastward into central Oregon, while Red-naped Sapsuckers have simultaneously retracted from central Oregon, resulting in movement of the hybrid zone (Howell 1952, Johnson and Johnson 1985).

To assess the influence interactions between sapsucker species may have on the moving hybrid zone, we tested 3 hypotheses related to differences in levels of aggressive behavior between Red-naped and Red-breasted sapsuckers: (1) Red-breasted Sapsuckers will be more aggressive than Red-naped Sapsuckers; (2) Red-breasted Sapsuckers will respond equally to conspecific and heterospecific stimuli, while Red-naped Sapsuckers will respond most strongly to conspecific stimuli; and (3) differences in aggressive responses will be stronger between sympatric populations than between allopatric populations. We tested our 3 hypotheses by quantifying the aggressive response of sapsuckers using a series of playback and taxidermic mount experiments on conspecific and heterospecific individuals in areas of sympatry and allopatry. To test our first hypothesis, we compared overall measures of aggressive responses. Based on previous observations, where Red-breasted Sapsuckers appeared to be more responsive to playback than Red-naped Sapsuckers while collecting data for genetic studies (S. M. Billerman, personal observation), the direction of hybrid zone movement with the expansion of Red-breasted Sapsuckers eastward, and the results of previous similar studies (e.g., Pearson and Rohwer 2000, McDonald et al. 2001), we predicted that Red-breasted Sapsuckers would show higher levels of aggression than Red-naped Sapsuckers. If Red-breasted Sapsuckers were displacing Red-naped Sapsuckers by preventing them from accessing territories or mates, such interspecific interactions could act as drivers of hybrid zone movement in this system. We tested our second hypothesis by assessing the aggressive responses of individuals toward simulated conspecific and heterospecific territory threats. If we find support for our first hypothesis and Red-breasted Sapsuckers are aggressively dominant, we also predict they would react equivalently toward conspecific and heterospecific taxidermy mounts. If Red-naped Sapsuckers were less aggressive and therefore subordinate to Red-breasted Sapsuckers, they might avoid conflict with the aggressively dominant Red-breasted Sapsucker, resulting in avoidance of heterospecific Red-breasted Sapsucker taxidermic mounts in our experiments (Jankowski et al. 2010, Seneviratne et al. 2012, Pasch et al. 2013). Finally, based on our predictions from our previous 2 hypotheses, we will test our third hypothesis by comparing responses of sapsuckers in sympatric and allopatric populations. Differences in the aggressive responses may be spatially dependent. For example, in Neotropical singing mice (*Scotinomys* sp.; Pasch et al. 2013) and in Neotropical songbirds (Jankowski et al. 2010), response to heterospecifics is dependent on proximity to a parapatric range boundary, where individuals used learned behaviors to inform their interactions. If behavioral differences are contributing to hybrid zone movement and Red-breasted Sapsuckers are more aggressive, Red-naped Sapsuckers should reduce their aggressive responses toward Red-breasted Sapsuckers, resulting in greater differences in aggression between the 2 species in the contact zone.

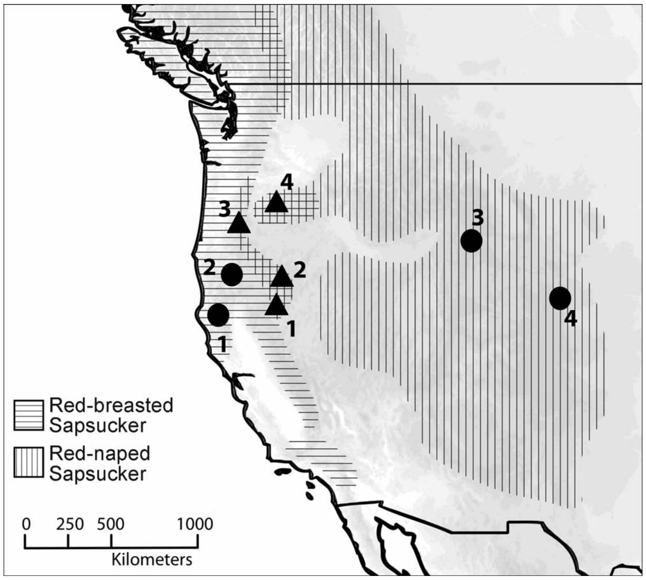

FIGURE 1. Map of the western United States and Canada showing the breeding distributions of Red-breasted (horizontal lines) and Red-naped (vertical lines) sapsuckers. The hybrid zone where the 2 species' ranges overlap is shown by cross-hatching. Localities where we collected data on aggressive behavior in sapsuckers are shown by circles (allopatric sites) and triangles (sympatric sites). Allopatric sites, with their respective sample sizes: (1) Trinity National Forest, $n = 26$; (2) Rogue River-Siskiyou National Forest, $n = 6$; (3) Bridger-Teton National Forest, $n = 7$; (4) Medicine Bow National Forest, $n = 14$. Sympatric sites, with their respective sample sizes: (1) Modoc National Forest, $n = 10$; (2) Fremont National Forest, $n = 49$; (3) Deschutes National Forest and Black Butte Ranch, $n = 9$; (4) Ochoco National Forest, $n = 5$.

METHODS

Study Area

Red-naped and Red-breasted sapsuckers are found in western North America, with Red-naped found through the Rocky Mountain region, and Red-breasted found farther west, from southern California north to southern Alaska (Figure 1). The 2 species come into contact from northeastern California north to southern British Columbia. We studied sapsuckers in sympatry at montane regions of northeastern California and central Oregon (Figure 1), where various aspects of the hybrid zone have been studied previously (Howell 1952, Johnson and Johnson 1985, Trombino 1998).

We sampled sympatric sapsuckers at 4 localities: Modoc National Forest in northeastern California (Modoc County; 41.96°N, 120.60°W), Fremont National Forest in south-central Oregon (Lake County; 42.44°N, 120.41°W), Deschutes National Forest and Black Buttes Ranch in central Oregon (Deschutes County; 44.36°N, 121.56°W and 44.37°N, 121.66°W, respectively), and Ochoco National Forest in central Oregon (Crook and Wheeler Counties; 44.33°N, 120.28°W) (Figure 1). We studied Red-breasted Sapsuckers in allopatry at 2 sites: Rogue River-Siskiyou National Forest in southwestern Oregon (Josephine County; 42.11°N, 123.39°W), and Trinity National Forest in northwestern California (Trinity County; 40.43°N, 123.44°W). We studied Red-naped Sapsuckers in allopatry at 2 localities in Wyoming: Bridger-Teton National Forest (Teton County; 43.83°N, 110.67° W) and Medicine Bow National Forest (Albany County; 41.20° N, 105.39°W) (Figure 1).

Taxidermic Mount Experiment

We used taxidermic mounts and playback to quantify the aggressive responses of sapsuckers in sympatry and allopatry. Taxidermic mounts were used to simulate a territorial intruder (Pearson and Rohwer 2000, Uy et al. 2009). Mounts were prepared of a single Red-naped and Red-breasted sapsucker from birds collected the previous year in Colorado and Oregon, respectively. Each specimen was an adult male in alternate plumage. We obtained recordings for playback experiments from the Macaulay Library at the Cornell Lab of Ornithology (see Appendix Table 6). We included 3 separate recordings of Red-naped Sapsuckers (of at least 2 individuals) and 2 recordings of Red-breasted Sapsuckers (of at least 2 individuals). Recordings were cut into multiple clips to remove unwanted portions (e.g., background noise, recorder comments, silent segments). We combined recordings of both species, with each clip created from the sapsucker recordings going into one playlist that we shuffled at random during playback. Calls and drums of each species are indistinguishable and not significantly different under most conditions (Trombino 1998, Walters et al. 2014a,b), and so were included together during playback. Because our objective was to test for an overall response difference, and not to parse out which aspects of territorial aggressive behavior were important to each species, we combined calls and drums into a single, randomized playlist. We also included both calls and drums because both are used in aggressive, territorial interactions in both Red-naped and Red-breasted sapsuckers (Walters et al. 2014a,b). We used an iPod Shuffle (Apple, Cupertino, California, USA) connected to an RP-SPT70 portable speaker (Panasonic, Kadoma, Japan) for playback in each experiment.

Within presumed territories of sapsuckers, we chose either Red-naped or Red-breasted sapsucker taxidermic mounts randomly, by flipping a coin, to quantify aggressive responses. Study sites were chosen based on field work from previous years, where we knew sapsuckers to occur within the area (S. M. Billerman and M. D. Carling, personal observations). Due to logistical constraints, and given the lack of response to noncompetitor controls in other studies (McDonald 1993, McDonald et al. 2001, Uy et al. 2009; but see Greig et al. 2015), and because we were interested primarily in the difference in responses between species, we chose not to use a noncompetitor mount to estimate baseline aggression levels. We conducted mount presentations between May 6 and June 5, 2013, while birds were still territorial but before feeding nestlings. Taxidermic mounts were attached to the end of 4.7-cm diameter PVC poles using plastic zip ties. PVC poles were made up of three 1-m long sections attached together for a total height of 3 m, and were painted brown to match the color of tree trunks. Poles (and mounts) were propped against the north side of trees and secured with bungee cords wrapped around the trunk of the tree. We chose trees with good visibility around them to ensure territorial sapsuckers could see the mount. Each taxidermic mount was attached to a lever with a monofilament string that allowed us to add small rocking movements to better simulate a living bird (Pearson and Rohwer 2000, Seneviratne et al. 2012). We used these movements to attract the attention of sapsuckers brought in by playback.

We monitored the behavior of sapsuckers for a period of 15 minutes (Pearson and Rohwer 2000). We used playback throughout the 15-min period a mount was in place to attract birds to the mount. We stopped recording the response of individual sapsuckers if they flew out of sight during our experiment, as we were unable to track behavior accurately at this point.

We scored 32 birds for their response to mount experiments in allopatric Red-breasted Sapsucker populations, 21 in allopatric Red-naped Sapsucker populations, and 74 birds in sympatric populations ($n = 60$ Red-breasted, $n = 7$ Red-naped, $n = 7$ hybrids). To quantify the aggressive responses of sapsuckers across our study area, we measured 6 aggressive response variables. We estimated, in meters, the closest distance birds approached the mount using the 1-m sections of PVC as reference. We recorded the time from the start of the 15-min period that birds reached each new distance from a mount (Pearson and Rohwer 2000, Uy et al. 2009). We measured the number of times a responding bird vocalized and drummed, as both may reflect an aspect of aggression (Walters et al. 2014a,b). Finally, we recorded whether birds physically attacked a taxidermy mount and whether a bird swooped at the mount.

We combined our estimates of the distance within which the birds approached mounts with physical attacks and swooping attacks, and converted these measures to an approach score to simplify analyses. Approach scores ranged from 1 to 7, and were quantified as follows: 1 = physical attack (0 m); 2 = swoop attack, where a bird dove at but never made physical contact with a mount; 3 = approach to less than 1 m of mount; 4 = approach between 1 and 3 m of mount; 5 = approach more than 3 m and up to 6 m of mount; 6 = approach greater than 6 m; 7 = appearance within our range of observation, typically just flying through or landing far from the mount, but not showing any further interest in the mount. We thus had 4 aggressive response variables that we used in our final analyses: an approach score, the time it took birds to reach the minimum distance from a mount, the number of times a bird called, and the number of times a bird drummed.

We used the phenotype of the birds whose aggressive responses we measured in sympatry in order to estimate ancestry and identify birds to species. We modified the hybrid index used by Johnson and Johnson (1985) to identify hybrids based on our own specimens collected across the hybrid zone. The extent of red plumage on the head, breast, and nape was used to identify birds to one of three categories: Red-breasted, Red-naped, or hybrid sapsucker. We identified Red-breasted Sapsuckers as having fully red breasts with no black feathering, a fully red nape and back of head with no black, and extensive red on the face such that the white malar was difficult to see. We identified Red-naped Sapsuckers as having a full black breast patch with a red throat, small red nape patch entirely surrounded by black feathers, nearly all black auricular patch, and a full white malar. Birds with hybrid phenotypes showed characteristics intermediate between Red-naped and Red-breasted sapsuckers, but generally showed the following traits: red breasts with extensive black feathering, small black nape patches entirely surrounded by red feathering, extensive red and black feathering on the auriculars, and an extensive white malar.

Data Analysis

We used our approach score, the total number of drums, the number of calls, and the time it took to reach the minimum distance from the mount to test for differences in the aggressive response of Red-naped and Red-breasted sapsuckers. Our full dataset consisted of 32 birds from allopatric Red-breasted populations, 21 from allopatric Red-naped populations, and 74 birds from sympatric populations ($n = 60$ Red-breasted, $n = 7$ Red-naped, $n = 7$ hybrids).

Correlation among aggressive response variables. We tested for significant associations among the 4 aggressive response variables to determine how each variable was related to the others, and to determine which response variables might represent different components of the aggressive response. We used a Pearson's correlation coefficient as implemented in R (R Core Development Team 2015).

Predictors of aggressive responses. For our analyses assessing the variables that have the greatest effect on the aggressive responses of sapsuckers, we used mixed models (Bolker et al. 2009, Uy et al. 2009, Jankowski et al. 2010, Pasch et al. 2013, Freeman 2016) as implemented in the "lme4" package (Bates et al. 2015) and the "ordinal" package (Christensen 2015) in R (R Core Development Team 2015). We chose to combine the counts of the number of calls and drums from an individual into a single measure of total acoustic aggression. We combined these measures into a single response variable for 2 reasons: (1) because they are significantly positively correlated (see Results); and (2) because our playback was a combination of calls and drums, there was no way to tease apart differences in the responses in these variables.

We used a generalized linear mixed model approach for assessing the important predictors of acoustic aggressive responses; we used a Poisson distribution fit by a Laplace approximation (Bolker et al. 2009, Pasch et al. 2013). We used a cumulative link mixed model, which uses an ordinal regression approach, to assess the important predictors of aggressive response as measured by our approach score (Christensen 2015). Lastly, we used a generalized linear mixed model to assess which explanatory variables best predicted how fast birds approached a mount; because our data was not distributed normally, we used a gamma distribution fit by a Laplace approximation (Bolker et al. 2009). For all of the models we constructed, we included 2 random effects. First, we included a random effect of sample site (defined by which National Forest the experiment was conducted in) to control for among-population and within-species variation in responses. Second, we included the number of individual sapsuckers responding to a given playback experiment as a random effect to control for variation due to the number of responding individuals. In some playback experiments, 2 or 3 individual sapsuckers responded to the playback during a single 15-min observation (mean number of birds responding across all experiments = 1.42, range = 1–3). In many cases, the second (or third) individual appeared to be an intruder to the territory and was chased from the study site by the original bird, at which point the original bird would no longer react to playback or the mount, effectively ending the trial. Multiple birds more commonly responded at sympatric sites ($n = 18$ experiments) than at allopatric sites ($n = 5$ experiments), possibly a result of a higher density of birds within the hybrid zone (S. M. Billerman, personal observation). For our acoustic aggression models, we included a third random effect: individual ID, to account for overdispersion of our acoustic aggression data.

For each of the 3 aggressive response variables, we constructed 3 independent models to test our 3 main hypotheses (Table 1). To test the first hypothesis, we included the identity of the species responding to the experiment and the 2 random effects (site and number of individuals responding, as well as a third, individual ID for acoustic aggression) in our model. To test our second hypothesis that species might respond differently depending on the identity of the mount treatment (i.e. simulated territory intruder), we included species identity, the mount treatment used in a given playback experiment, an interaction term of species and mount treatment in our model, and the random effects. Finally, to test our third hypothesis that aggressive responses would be different between populations, we included the identity of the species, whether the experiment took place in the zone of sympatry or in allopatric populations, an interaction term of species and location of the experiment in our model, and the random effects (Table 1). We also constructed a fourth, global model that included all explanatory variables included to test whether all of our variables together contributed to explaining the aggressive responses of sapsuckers.

We included hybrid individuals only in the first model testing the effect of responding species on the aggressive response. Because hybrids occur only in sympatric populations, we were unable to test for an effect of whether birds were sampled from allopatric or sympatric populations.

TABLE 1. Descriptive table showing each of our 3 models to test each of our 3 hypotheses, plus a global model with all explanatory variables. Table shows the explanatory variables included in each model to test each of our hypotheses. All 4 models had the same 2 random effects: (1) number of responding individuals to a given experiment; and (2) location, which corresponds in our study to the National Forest where each playback experiment was conducted.

Hypotheses	Model	Random effects
(1) Red-breasted Sapsuckers are more aggressive	Aggressive response $\sim$ Species identity	(1) Number of responding individuals, (2) Location
(2) There is an effect of mount treatment on the aggressive responses of sapsuckers	Aggressive response $\sim$ Species $+$ Mount treatment $+$ (Species identity * Mount treatment)	(1) Number of responding individuals, (2) Location
(3) There is an effect of whether birds were sampled in sympatry or allopatry	Aggressive response $\sim$ Species $+$ Location relative to hybrid zone $+$ (Species * Location relative to hybrid zone)	(1) Number of responding individuals, (2) Location
(4) Global Model	Aggressive response $\sim$ Species $+$ Mount treatment $+$ (Species * Mount treatment) $+$ Location relative to hybrid zone $+$ (Species * Location relative to hybrid zone)	(1) Number of responding individuals, (2) Location

For each of the models for each of the 3 aggressive response variables, we compared model support using second-order Akaike's Information Criterion ($\mathrm{AIC_c}$; Burnham and Anderson 2002) values to determine which model best fit our data using both the "AICcmodavg" (Mazerolle 2016) and the "MuMIn" packages (Bartón 2016), as implemented in R (R Core Development Team 2015). We used predictions from the best-fitting model, including 95% CIs, to examine and aid in interpretation of interaction effects. Predictions were calculated without specifying levels of the random effects, providing a more generalizable, population-level prediction of the fixed effects (Bolker et al. 2009). We calculated confidence intervals using a parametric bootstrapping approach, which bootstrapped predictions by resampling, refitting, and re-predicting values for 500 iterations (Bolker et al. 2009).

RESULTS

Correlation among Aggressive Response Variables

Some of our aggressive response variables were significantly correlated (Table 2). We found that the number of times a bird called and drummed were significantly positively correlated ($r = 0.39$, $p < 0.001$). We also found that the time it took a bird to reach its closest distance to a mount was significantly negatively correlated both with the number of times a bird drummed and the closest a bird approached a mount ($r = -0.26$ and -0.34, respectively; $p = 0.003$ and $p < 0.001$, respectively).

Predictors of Aggressive Responses

Using a mixed modeling approach, we found that there were differences in the aggressive responses between Red-naped and Red-breasted sapsuckers. There were significant differences between species for 2 of our 3 aggressive response variables. We also found that location relative to the hybrid zone and mount treatment had significant effects on the aggressive responses of sapsuckers. All effect sizes are predicted from our models and are reported as means and 95% confidence intervals. Hybrid individuals did not have a significant effect on our aggressive response variables, so we only report results for models without hybrids.

Acoustic Aggression

Using a generalized linear mixed model, we found that Red-naped Sapsuckers had higher levels of acoustic aggression, and were more likely to call and drum compared with Red-breasted Sapsuckers (Red-naped: 9.6 [4.0–23.3], Red-breasted: 0.6 [0.3–1.2], Wald $z = -4.2$, $p = 0.001$). The top-ranked model, testing Hypothesis 1 (Table 1), included only the identity of the responding species (Figure 2A). While the top-ranked model only included species identity, the model that included mount treatment and an interaction between mount treatment and the species responding, which tested Hypothesis 2 (Table 1), had a $\Delta\mathrm{AIC_c}$ score of 1.15 and a cumulative Akaike weight (w_i) of 0.88 (Table 3), suggesting it is equivalent to the top-ranked model (Burnham and Anderson 2002). In our model testing Hypothesis 2, species identity and mount

TABLE 2. Correlation matrix showing the Pearson's correlation coefficient (*r*) between 4 aggressive response variables measured in sapsuckers. Correlation coefficients among response variables are shown above the diagonal. *P*-values are shown below the diagonal. Significant values, as assessed by $\alpha < 0.05$, are italicized.

	Distance score	Time to response	Calls	Drums
Distance score	–	–0.35	0.09	0.02
Time to response	*<0.001*	–	–0.13	–0.26
Calls	0.33	0.14	–	0.39
Drums	0.81	*0.003*	*<0.001*	–

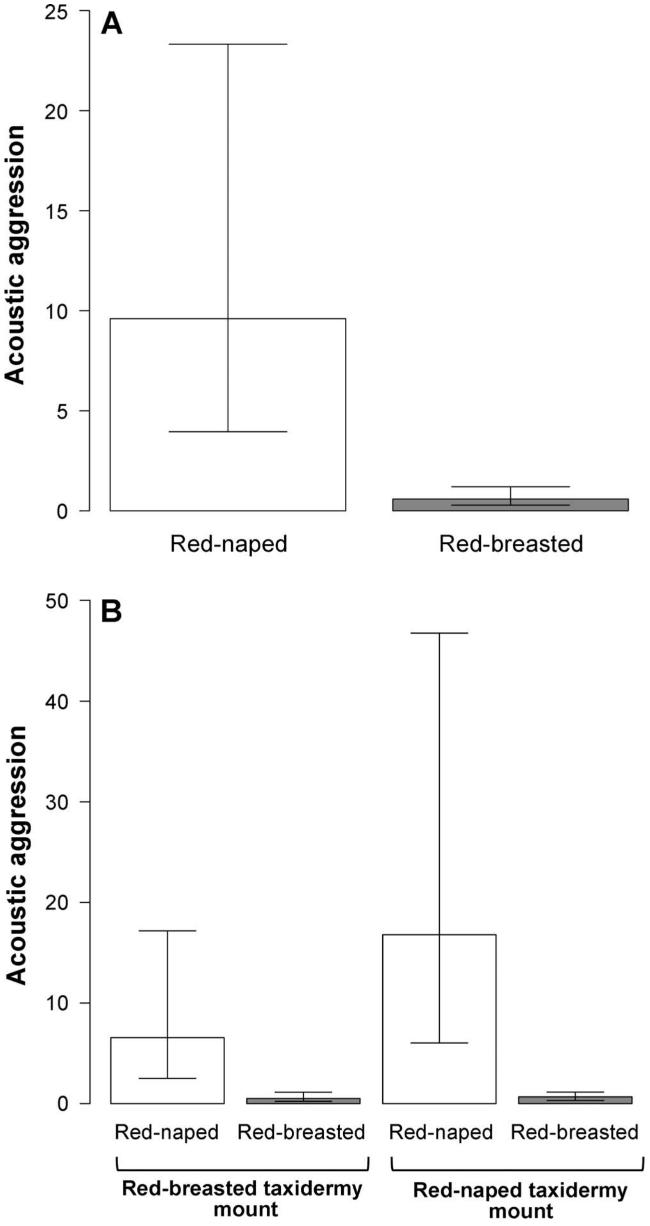

FIGURE 2. Bar plots showing the predicted acoustic aggression from our top-ranked models. (**A**) Predicted count of acoustic aggression for Red-naped and Red-breasted sapsuckers. We found that Red-naped Sapsuckers called and drummed more than Red-breasted Sapsuckers. (**B**) Predicted count of acoustic aggression for Red-naped and Red-breasted sapsuckers in response to each taxidermy mount treatment (Red-breasted Sapsucker taxidermy mount on left, Red-naped Sapsucker taxidermy mount on right). We found Red-naped were significantly more acoustically aggressive than Red-breasted Sapsuckers. Red-naped Sapsuckers had higher levels of acoustic aggression in response to the Red-naped Sapsucker taxidermy mount than in response to the Red-breasted Sapsucker taxidermy mount. Error bars represent the 95% confidence interval for each predicted value as calculated using a bootstrap of the model output (500 iterations).

TABLE 3. Second-order Akaike's Information Criterion (AIC_c) table for acoustic aggression generalized linear mixed models. Included in the table are the number of parameters included in the model (*K*), the second-order AIC (AIC_c), the delta-AIC (ΔAIC_c), and Akaike weights, or model probabilities (w_i). Table includes models testing each of our 3 hypotheses for our acoustic aggressive response variable (see Table 1), as well as a global model that includes all explanatory variables. Models are listed from top-ranked to lowest-ranked.

Acoustic aggression	*K*	AIC_c	ΔAIC_c	w_i
Hypothesis 1	5	552.35	0.00	0.56
Hypothesis 2	7	553.49	1.15	0.32
Hypothesis 3	7	556.41	4.07	0.07
Global model	9	557.36	5.02	0.05

treatment had an effect on the acoustic aggressive response. Red-naped Sapsuckers had higher levels of acoustic aggression compared with Red-breasted, with mean aggression levels predicted from our model ranging from 6.55 to 16.79 in response to heterospecific versus conspecific mounts. Red-breasted Sapsuckers, by comparison, showed a range of acoustic aggression values of 0.51 to 0.68 in response to conspecific versus heterospecific mounts (Figure 2B). While Red-naped Sapsuckers had higher levels of aggressive response toward the conspecific mount treatment, the 95% confidence intervals overlapped with those of the predicted values for the response to the heterospecific mount (Figure 2B). In the models that included position relative to the hybrid zone, there was not an effect of whether birds were sampled in sympatry versus allopatry, with birds having equivalent aggressive responses in both allopatry and sympatry.

Approach Score

To test the effect of species, mount treatment, and location relative to the hybrid zone on the minimum distance individuals approached a mount, we used a cumulative link mixed model (Christensen 2015). We found that no explanatory variable in any of the 4 models (species only, species and mount treatment interaction, species and hybrid zone interaction, full model) had a significant effect on the minimum distance birds approached a mount. Red-naped and Red-breasted sapsuckers showed similar levels of aggressive response as measured by the approach score. We found that Red-naped Sapsuckers had a mean approach score of 3.88 and Red-breasted had a mean score of 3.54, indicating that Red-breasted Sapsuckers showed slightly higher levels of aggression than Red-naped using this measure. However, there was extensive overlap in the 95% confidence intervals, suggesting that the effect size was small, and that approach scores were equivalent between species. Though no model contained variables that had an effect on approach score, we did find that the model that included only the identity of the responding

TABLE 4. Second-order Akaike's Information Criterion (AIC_C) table for approach score cumulative link mixed models. Included in the table are the number of parameters included in the model (*K*), the second-order AIC (AIC_C), the delta-AIC_C (ΔAIC_C), and Akaike weights, or model probabilities (w_i). Table includes models testing each of our 3 hypotheses for our distance score response variable (see Table 1), as well as a global model that includes all explanatory variables. Models are listed from top-ranked to lowest-ranked.

Distance score	*K*	AIC_c	ΔAIC_c	w_i
Hypothesis 1	4	399.85	0.00	0.81
Hypothesis 3	6	404.15	4.30	0.09
Hypothesis 2	6	404.3	4.45	0.09
Global model	8	408.93	9.08	0.01

TABLE 5. Second-order Akaike's Information Criterion (AIC_C) table for time to closest approach linear mixed models. Included the table are the number of parameters included in the model (*K*), the second-order AIC (AIC_C), the delta-AIC (ΔAIC_C), and Akaike weights, or model probabilities (w_i). Table includes models testing each of our 3 hypotheses for our time to closest approach response variable (see Table 1), as well as a global model that includes all explanatory variables. Models are listed from top-ranked to lowest-ranked.

Time to response	*K*	AIC_c	ΔAIC_c	w_i
Hypothesis 1	5	1595.29	0.00	0.57
Hypothesis 3	7	1597.17	1.88	0.22
Hypothesis 2	7	1597.76	2.47	0.17
Global model	9	1600.62	5.32	0.04

species was our top-ranked model (Table 4), representing our test of Hypothesis 1 (Table 1).

Time to Response

Using generalized linear mixed models, we found that the simplest model, which included only the identity of the responding species testing Hypothesis 1 (Table 1), was the top-ranked model (Table 5). We found that Red-naped Sapsuckers approached mounts 109.7 s faster than Red-breasted based on model predictions (Red-naped: 276.5 s [216.2–383.4 s], Red-breasted: 386.2 s [323.0–480.2 s], $t = -1.50$; Figure 3A). There was, however, overlap in the 95% confidence intervals of these predictions. While the top-ranked model included only species identity, the generalized mixed model that included hybrid zone position, testing Hypothesis 3 (Table 1), had a ΔAIC_c score of 1.88 and a cumulative w_i of 0.79 (Table 5), suggesting it is equivalent to the top-ranked model (Burnham and Anderson 2002). Using this model, we found that Red-naped Sapsuckers made their closest approach to mounts faster in allopatric populations than in sympatric populations (Figure 3B), approaching mounts an average of 1.7 times faster in allopatric populations than in sympatric populations. Sympatric Red-naped populations approached mounts similarly to both allopatric and sympatric Red-breasted populations (Figure 3B). The other models also suggest an important influence of mount treatment used, with a significant effect of both mount treatment and a mount treatment / species identity interaction, although both models that included these terms were not as well supported (Table 5).

DISCUSSION

In our assessment of aggressive response differences between 2 species of sapsucker that form a hybrid zone, we found, counter to our expectations, that Red-breasted Sapsuckers were not more aggressive than Red-naped Sapsuckers. Instead, we found the opposite: Red-naped Sapsuckers were more aggressive than Red-breasted. Our results argue against the importance of interspecific aggressive behavior as a major driver of hybrid zone dynamics (as in Pearson and Rohwer 2000, McDonald et al. 2001, Krosby and Rohwer 2009, 2010). Using taxidermic mounts and playback, we reject 2 of our 3 hypotheses outright: (1) contrary to our hypothesis, Red-naped Sapsuckers were more aggressive than Red-breasted; and (2) differences in aggressive responses were not strongest in sympatric populations, with sympatric populations of both species instead showing equivalent responses. We show that where they differed, Red-naped Sapsuckers had higher levels of acoustic aggression, and also responded to taxidermic mounts and playback more quickly than Red-breasted. Finally, we found that Red-naped Sapsuckers differed in their response to conspecific taxidermic mounts than they did to heterospecific mounts, being more acoustically aggressive and approaching conspecific mounts faster.

Antagonistic behaviors in many woodpecker species consist of physical interactions, including chasing and physical attacks, and various vocalizations (Lawrence 1967, Brenowitz 1978, Walters et al. 2014a,b). For instance, vocalizations, including drumming and calling, may be important aspects of aggression that signal territory ownership to intruders. Vocal signals may also accompany other visual displays of aggression toward intruders (Lawrence 1967, Walters et al. 2014a,b). We found that the number of times a bird called and drummed (acoustic aggression; Table 2), did differ between Red-breasted and Red-naped sapsuckers in our study. Contrary to our predictions, Red-naped Sapsuckers were more acoustically aggressive than Red-breasted, which may reflect a difference in a part of aggressive behavior between these 2 species. Calling and drumming may be an especially important signal to Red-naped Sapsuckers and how they respond to and assess threats (Akçay et al. 2015), while Red-breasted Sapsuckers may rely more on visual cues to assess territory threats, such as head bobbing, wing

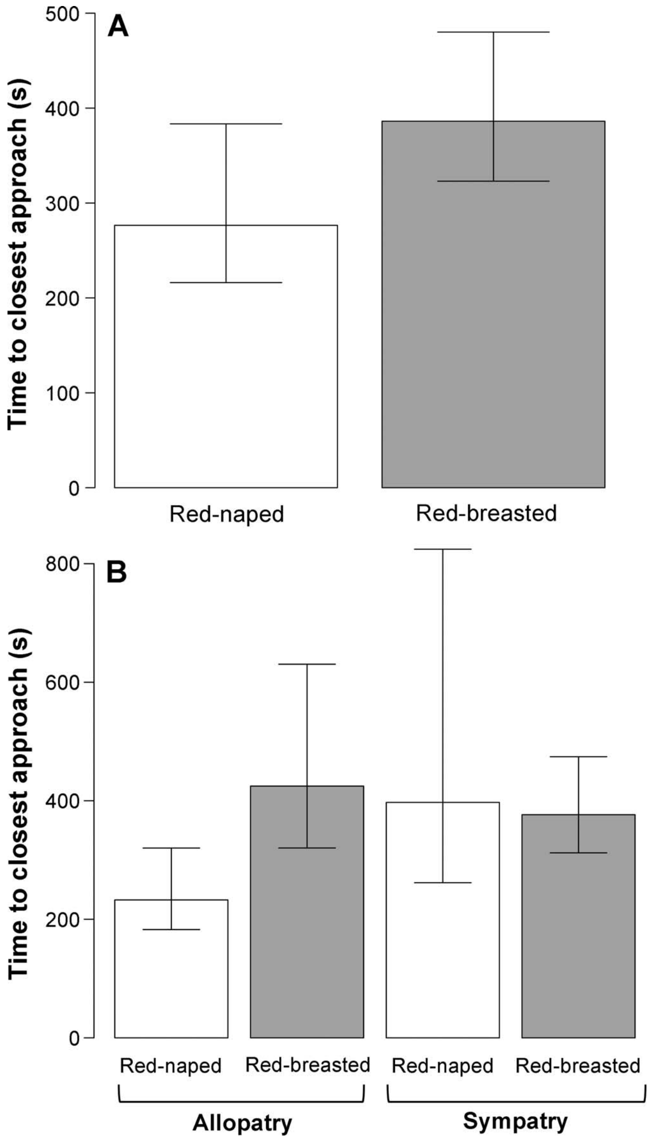

FIGURE 3. Bar plots showing the predicted time to closest approach (in seconds) for Red-naped and Red-breasted sapsuckers from our top-ranked models. (**A**) We found Red-naped Sapsuckers approached mounts significantly faster than Red-breasted Sapsuckers. (**B**) The predicted time to closest approach (in seconds) for Red-naped and Red-breasted sapsuckers from allopatric populations (left) and sympatric populations (right). We found Red-naped Sapsuckers approached mounts faster than Red-breasted Sapsuckers, and approached mounts significantly faster in allopatric populations compared to all Red-breasted Sapsucker populations and Red-naped Sapsuckers from sympatric populations. Error bars represent the 95% confidence interval for each predicted value as calculated using a bootstrap of the model output (500 iterations).

flicking, and tail spreading (Walters et al. 2014a). The difference in the aggressive responses that we identified may hint at species-specific differences in aggression that were not captured in our study design. However, our inability to replicate ritualized physical behaviors, such as head bobbing and tail spreading, using taxidermic mounts may have limited our ability to observe the full range of antagonistic responses from Red-naped and Red-breasted sapsuckers.

Although we detected differences in aspects of the aggressive responses of sapsuckers, we were unable to identify a difference in aggressive behaviors that resulted in physical attack. We argue that physical aggression might be more important in structuring hybrid zones and contributing to movement of the contact zone (Lawrence 1967, Reller 1972, Brenowitz 1978, Pearson and Rohwer 2000, McDonald et al. 2001, Walters et al. 2014a,b). For example, a study comparing the aggressive behavior of territorial Red-headed (*Melanerpes erythrocephalus*) and Red-bellied (*M. carolinus*) woodpeckers found that differences in the aggressive responses manifested most strongly in physical interactions that involved chasing and displacement behaviors (Reller 1972), suggesting that in the context of our hybrid zone, differences in calling may not be an important mechanism in driving shifts of the contact zone. In 2 other hybrid systems where aggression plays a role in movement, physical interactions were important aspects of the aggressive response, where the dominant species that is expanding physically attacked the subordinate species (Pearson and Rohwer 2000, McDonald et al. 2001).

In addition to detecting overall differences in aggressive behavior between species, we also predicted that differences in the aggressive responses of sapsuckers would be most apparent in sympatry, either a result of character displacement (Trombino 1998, Grether et al. 2009) or a learned response to aggressive individuals in areas where the species overlap (Jankowski et al. 2010, Pasch et al. 2013). However, we rejected our hypothesis that aggressive differences between species would be greater between sympatric populations, finding no significant differences in any of our measures of aggression between species at sympatric sites. Though we found no differences between species in sympatry, we did find that Red-naped Sapsuckers showed higher levels of aggression (as measured by time to approach a mount) in allopatry than in sympatry (Figure 3B), approaching on average 164.7 s faster in allopatric populations than in sympatric populations. This finding may support our prediction that sapsuckers (specifically Red-naped) modulate their aggressive responses when in the presence of Red-breasted Sapsuckers, such that they match their aggression levels in sympatry and avoid elevated aggressive interactions, but are more aggressive in allopatry. However, the patterns of reduced aggression of Red-naped Sapsuckers in sympatry relative to allopatric populations may be due to other factors. For instance, due to movement of the Red-naped and Red-breasted sapsucker hybrid zone in Oregon and California, our sample size of Red-naped Sapsuckers in the contact zone is small. Throughout much of the contact zone in our study area, Red-naped Sapsuckers no longer persist, with the contact zone instead dominated by Red-breasted Sapsuckers and birds showing hybrid phenotypes (S. M. Billerman and M. D. Carling, personal observations). The shifts in the distributions of Red-naped and Red-breasted sapsuckers in the contact zone have resulted in a situation where there are no localities within the hybrid zone where Red-naped Sapsuckers are common. Change within the hybrid zone may have influenced our ability to assess the differences in aggression in sympatry by reducing the number of Red-naped Sapsuckers we were able to sample.

We found mixed support for our second hypothesis. We did find evidence for differences in how sapsuckers responded aggressively toward conspecifics and heterospecifics. Specifically, we predicted that Red-breasted Sapsuckers would be equally aggressive toward all individuals, while Red-naped would avoid interacting with competitively dominant heterospecifics. In our models of acoustic aggression, a top-ranked model found that Red-naped Sapsuckers called and drummed more than twice as much (average of 10 more calls and drums) toward a conspecific taxidermic mount than toward a heterospecific mount, in support of our second hypothesis (Table 1, Figure 2B). Red-breasted Sapsuckers, however, did not differ in their responses toward either conspecific or heterospecific individuals. In another set of models investigating the factors affecting time to closest approach, we found an effect of mount-treatment on response time. Though not a top-ranked model (Table 5), we did find that Red-naped Sapsuckers responded faster toward conspecific mounts than to a heterospecific mount. There was extensive overlap of confidence intervals of these values, so effect size from the model was predicted to be small. These results may suggest some avoidance of Red-breasted Sapsuckers by Red-naped. However, even though Red-naped Sapsuckers showed reduced aggression toward heterospecific mount treatments relative to conspecific treatments, their overall aggressive responses (in both acoustic aggression models and time to closest approach models) were still higher than the aggressive responses of Red-breasted Sapsuckers. These results may be similar to results in British Columbia where Red-breasted Sapsuckers avoided interactions with Yellow-bellied Sapsucker mounts (Seneviratne et al. 2012). In British Columbia, individuals recognized species and perceived the threats they posed differently, and adjusted their aggressive response. However, our results may also suggest a scenario where Red-naped Sapsuckers do not perceive Red-breasted as a territorial threat in the same way that they perceive another Red-naped intruder. Patterns of mate choice in the hybrid zone may help address this pattern further, where evidence suggests there is assortative mating between sapsucker species (Howell 1952, Johnson and Johnson 1985, Trombino 1998). If there is assortative mating, Red-naped Sapsuckers may not consider Red-breasted Sapsuckers a threat to either their territory or mate. Additional work would be needed to further explore these results and to better understand how threats are assessed by Red-breasted and Red-naped sapsuckers.

In a hybrid zone in British Columbia between Yellow-bellied and Red-breasted sapsuckers, Yellow-bellied were significantly more physically aggressive toward heterospecific taxidermic mounts (Seneviratne et al. 2012). There is also evidence that the hybrid zone has shifted to the west, with Yellow-bellied Sapsuckers expanding their range, suggesting that aggressive behavior may play a role in this moving hybrid zone (Seneviratne et al. 2012). Although Red-naped and Red-breasted sapsuckers did differ in aspects of their aggressive response, the differences we observed in acoustic aggression and timing of their aggressive response are likely not contributing to hybrid zone movement like aggressive differences may be in the Yellow-bellied and Red-breasted sapsucker hybrid zone in British Columbia (Seneviratne et al. 2012). If the differences in aggressive behavior we observed between Red-naped and Red-breasted sapsuckers were important mechanisms for hybrid zone movement, the hybrid zone should be moving west, not east like we find (Howell 1952, Johnson and Johnson 1985). Instead, we suggest that climate is the primary driver of hybrid zone movement in our system based on evidence from Billerman et al. (2016). The aggressive responses we documented likely serve a different function in the hybrid zone we studied in Oregon and California than they do between sapsuckers in British Columbia (Seneviratne et al. 2012). For example, Scordato (2012) found differences in patterns of inter-male competition across the distribution of Greenish Warblers (*Phylloscopus trochiloides*) from India to Russia in response to different selection pressures. Where resources were limited and breeding densities were high in the southern part of their range, warblers were aggressive all year round and defended females. Farther north, however, where resources were high and breeding densities low, males were only territorial and competitive early in the breeding season when territories were established (Scordato 2012). We know little about resource availability and selection pressures for sapsuckers in Oregon and California, but we have observed that aggressive responses drop off substantially once chicks hatch (S. M. Billerman, personal observation). We suggest that aggression may only serve to establish territories between Red-naped and Red-breasted sapsuckers in Oregon and California, and may not be important in mate defense or resource defense post territory establishment as it might be farther north in British Columbia between Red-breasted and Yellow-bellied Sapsuckers (Seneviratne et al. 2012).

In addition to potential differences in how aggressive behavior contributes to different sapsucker hybrid zones and taxa, we also see striking differences in overall hybrid zone dynamics between different sapsucker systems. In both the Red-naped and Yellow-bellied hybrid zone, and the Red-naped and Red-breasted hybrid of British Columbia, data suggest that hybrid zones are relatively stable with little change over time (Howell 1952, Grossen et al. 2016, Seneviratne et al. 2016; but see Scott et al. 1976). In addition, the authors report that hybrids are much more scarce, suggesting there may be greater selection against hybrids (Scott et al. 1976, Grossen et al. 2016, Seneviratne et al. 2016). These differences among sapsucker hybrid zones may be due to differences in the contribution of aggressive behavior, as in Seneviratne et al. (2012), or may be due to different influences of climate and habitat structure. Given the strong role climate may play in changes to the Red-naped and Red-breasted sapsucker hybrid zone in California and Oregon (Billerman et al. 2016), differences in the importance of climate to each system could be influencing the relative contribution of aggressive behavior to hybrid zone movement. In models of range limits and the influence of interspecific interactions, Price and Kirkpatrick (2009) found that competition with other species could prevent range expansion into new niches, potentially leading to local extinctions. Despite the apparent higher levels of aggression in Red-naped Sapsuckers, they occupy a more restricted and declining niche (relatively cooler and drier conditions dominated by quaking aspen *Populus tremuloides*; Rehfeldt et al. 2009, Hanna and Kulakowski 2012, Walters et al. 2014b), while Red-breasted Sapsuckers occupy a broader niche (wide range of temperature and precipitation conditions and wide range of forest types; Billerman et al. 2016). Under these conditions, Red-naped Sapsuckers may continue to decline even with an aggressive advantage because there is no open niche for them to switch to or adapt to (see Price and Kirkpatrick 2009).

While we did not find support for our hypothesis that differences in aggressive behavior have contributed to changes in the sapsucker hybrid zone as in other systems (e.g., Pearson and Rohwer 2000, McDonald et al. 2001), we cannot rule out the possible influence of other behavioral differences. In particular, differences in mate choice patterns may result in changes to the Red-naped and Red-breasted sapsucker hybrid zone. Although there is strong evidence suggesting that assortative mating predominates in this hybrid zone (Howell 1952, Johnson and Johnson 1985, Trombino 1998), Johnson and Johnson (1985) also report that of all the interspecific pairs they documented, nearly 90% were between male Red-breasted Sapsuckers and female Red-naped Sapsuckers. Based on these observations, they hypothesize that when they do hybridize, female Red-naped Sapsuckers prefer males with more red in the plumage (Johnson and Johnson 1985). While we were unable to test for this possibility here, other research did not find evidence for selection for red contributing to changes of this hybrid zone (S. M. Billerman and M. D. Carling, personal observations).

Species interactions (Bronson et al. 2003, Engler et al. 2013), and specifically aggressive behavior, can influence hybrid zone structure and movement (Pearson and Rohwer 2000, McDonald et al. 2001, Krosby and Rohwer 2009, 2010). Even in some sapsucker hybrid zones, differences in aggressive responses may be contributing to hybrid zone structure (Seneviratne et al. 2012). We contribute to the collection of studies assessing the importance of species interactions in hybrid zone dynamics. Although we found differences in the aggressive behavior between Red-naped and Red-breasted sapsuckers, with Red-naped having significantly higher levels of acoustic aggression compared to Red-breasted, these differences were not consistent with our predictions, thus species interactions are unlikely to contribute to hybrid zone movement. Our findings also highlight the independence of different hybrid systems, with heterogeneity in the outcome of hybridization in different parts of the ranges of species (Seneviratne et al. 2012, Mandeville et al. 2015, Grossen et al. 2016, Seneviratne et al. 2016).

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Ethics statement: Our work was approved by and done in accordance with the University of Wyoming Institutional Animal Care and Use Committee. We also followed the University of Wyoming's Code of Ethical Conduct.

Author contributions: SMB designed the study, collected the data, completed analysis, interpreted the data, and wrote the paper. MDC designed the study, interpreted the data, and wrote the paper.

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APPENDIX TABLE 6. Data from audio recordings used in playback experiments from the Macaulay Library, Cornell Lab of Ornithology, including species, Macaulay Library catalog number, recordist, specific locality, state, and date the recording was made.

Species	Scientific name	Catalog number	Recordist	Specific locality	State	Date
Red-naped Sapsucker	*Sphyrapicus nuchalis*	63053	David S. Herr	Elgin, Phillips Creek	Oregon	April 11, 1992
Red-naped Sapsucker	*Sphyrapicus nuchalis*	63060	David S. Herr	Elgin, Phillips Creek	Oregon	April 10, 1992
Red-naped Sapsucker	*Sphyrapicus nuchalis*	63073	David S. Herr	4.0 km SW of Tollgate, Mcdougall Road	Oregon	April 15, 1992
Red-breasted Sapsucker	*Sphyrapicus ruber*	119418	Geoffrey A. Keller	27.4 km NW of Kernville, Sequoia National Forest, Holy Meadow Campground	California	May 30, 2001