

A COMPARISON OF INTER- AND INTRASPECIFIC AGGRESSION IN SYMPATRIC
POPULATIONS OF EASTERN (*TYRANNUS TYRANNUS*) AND WESTERN (*TYRANNUS*
VERTICALIS) KINGBIRDS

By EDWIN HARRIS¹

¹Beloit College, Department of Biology, Beloit, WI 53511

Abstract

Tyrant flycatchers (Family *Tyrannidae*) are known for their aggression and intense nest defense. Predation pressure, risk of paternity loss to extrapair fertilizations, and interspecific competition have all been proposed as explanations for these traits. In this study, intensity of intra- and interspecific aggression were compared between Eastern (*Tyrannus tyrannus*) and Western (*Tyrannus verticalis*) kingbirds at a site in Western Montana. Due to differing nest site preferences between the species, interspecific aggression was expected to be limited, as microhabitat divergence may alleviate competitive pressure. Conspecific, heterospecific kingbird, and Western meadowlark (*Sturnella neglecta*) calls were presented, and Eastern and Western kingbird responses were recorded. Eastern kingbirds exhibited the highest frequency of aggressive behaviors in response to conspecific calls, followed by Western kingbird calls. Western kingbirds responded with higher frequency of aggressive behaviors to kingbirds regardless of species. Given the greater abundance of Eastern kingbirds at this site, these results may indicate that competition from Eastern kingbirds is a greater perceived threat to both species than competition from Western kingbirds.

Key Words: Eastern kingbird; intraspecific competition; interspecific competition; Western kingbird

Introduction

The degree to which competition determines species distribution compared to resource availability, predation, and other ecological factors has been much debated within ecology (Sih et al. 1985, Saetre et al. 1999, Chase et al. 2002, Carrete et al. 2006). In cases where sympatric species have largely overlapping ecological requirements, competition for shared resources is expected to limit the reproductive output of the less effective competitor, leading to competitive

exclusion, or the local extinction of the 'subordinate' species, in cases where interspecific competition is more limiting than intraspecific competition (Saetre et al. 1999, Carrete et al. 2006). Interspecific competition is typically expected to be more intense among closely related sympatric species than among more evolutionarily distant species because related competitors are likely to have similar ecological needs (Saetre et al. 1999, Vallin et al. 2012).

Regional coexistence (on at least a temporary basis) of species that would be expected to undergo competitive exclusion under model conditions is often observed, indicating that other factors may limit the effects of competition, or that adaptive processes may prevent exclusion (Vallin et al. 2012). Temporal displacement, or the use of resources or territories at different times, is one mechanism that may reduce interference competition within an area (Cotton 2008). Use of different parts of a shared resource, or different strategies for obtaining a resource may also extend coexistence among potential competitors; for example, some species of flycatchers reduce competition for insect prey by hunting different sizes or ages of shared prey types, foraging at different heights, and using different hunting strategies than sympatric species of the same genus (Verbeek 1975).

Interspecific competition can be affected by habitat or environment features in addition to affecting distribution within an environment (Maher 2000). Food availability is a commonly studied environmental factors that may limit or favor competition: at very low food abundance, interference competition may be inhibited by low energy availability, while at high abundance, the costs of competition may outweigh the benefits (Maher 2000). Habitat heterogeneity may allow potential competitors to coexist by facilitating divergent microhabitat use within a shared landscape, while a simple habitat structure may prevent divergence of feeding strategies or habitat use, intensifying competition (Rohwer 1973, MacKenzie 1979, Jankowski et al. 2010).

Furthermore, if weaker competitors are more resilient to harsh environmental conditions, especially if competition induces higher energetic costs in the dominant competitor, they may persist despite the pressure of competition (Qvanstrom et al. 2005).

Competition and Aggression in Tyrant Flycatchers (Family Tyrannidae)

Eastern kingbirds (*Tyrannus tyrannus*) and Western kingbirds (*T. verticalis*), two species of tyrant flycatcher, are sympatric over large portions of their respective North American breeding ranges (MacKenzie and Sealy 1981). Like others of their genus, they are known for their aggressive behavior, territoriality, and intense parental defense (Smith and Smith 1992, Redmond et al. 2009). While one species will typically be much more abundant in a given area than the other, populations of Eastern and Western kingbirds appear to coexist at least at some studied locations (MacKenzie 1979, MacKenzie and Sealy 1981). Divergence in nest site preference could explain why competitive exclusion may not occur in areas of sympatry: Eastern kingbirds tend to nest at intermediate heights in trees, often at the edges of marshes and woodlands, or in riparian areas, while Western kingbirds are usually found in dry grasslands, and nest high in larger, more isolated trees or on anthropogenic structures (MacKenzie and Sealy 1981, Murphy 1983, 2001). Western kingbirds have been observed arriving to breeding grounds slightly before their Eastern counterparts, which may further reduce direct competition during nest site selection (MacKenzie and Sealy 1981).

Given the factors that may limit interspecific competition between Eastern and Western kingbirds, predation pressure is a common explanation for their aggressive behavior (Murphy 1983, Murphy et al. 1997). Although they may have higher rates of nest success than relatively less aggressive birds like cedar waxwings (*Bombycilla cedrorum*), rates of nest failure due to depredation at a site in Eastern Oregon were found to be independent of the intensity of nest

defense (Murphy et al. 1997, Redmond et al. 2009). Furthermore, kingbirds are frequently aggressive toward non-nest predators indicating that predation alone may not explain their intense defensive behaviors (Murphy et al. 1997). Although they may prefer different nest sites, particularly in heterogeneous habitats, aggressive interactions among flycatchers may be common at shared resource patches such as watering sites, potentially supporting interspecific competition as a factor in flycatcher aggression (Markova and Serebryakov 2016). Intraspecific competition may also motivate some aggressive behaviors in kingbirds. In one population, 60% of male Eastern kingbirds lost at least some paternity of their nest to extrapair fertilizations, and 25% lost all paternity (Redmond et al. 2009). Aggression toward intruders during the breeding season could reduce loss of paternity (though rates of extrapair paternity have been found to be independent of intensity of nest defense), or could be used by females as a signal of male quality, and be favored in sexual selection (Dolan et al. 2007, Redmond et al. 2009).

In this study, I wish to assess the intensity of aggression exhibited by Eastern and Western kingbirds in response to simulated conspecific, heterospecific kingbird, and heterospecific non-kingbird challengers in sympatric populations at the National Bison Range, a bunchgrass Palouse prairie in Western Montana. Examining the behavioral responses of Eastern and Western kingbirds may provide further context in understanding their distribution within a landscape that is not present in analyses of their habitat preferences alone. Although intensity of aggressive response is not a perfect substitute for intensity of competition, and intensity of competition itself may not account for the relative importance of competition in determining distribution or population dynamics, assessing whether either Eastern or Western kingbirds responds asymmetrically to different challengers may indicate the relative level of “threat” presented by heterospecific challengers compared to conspecific ones (Welden and Slauson 1986).

Although competitive exclusion does not appear common between Eastern and Western kingbirds in sympatric populations, the expansion of Western kingbird range in association with the planting of trees and construction of buildings in grasslands potentially introduces them to new competitive interactions with different species or previously allopatric populations (MacKenzie and Sealy 1981). As the range of various flycatchers shifts due to climate change, habitat fragmentation, land use changes, and so on, new interspecific interactions may occur; quantifying intra- and interspecific aggression, and comparing aggression levels in different species with overlapping ranges may help to understand future community changes resulting from novel range overlap in populations that did not have previous contact.

By exposing Eastern and Western kingbirds to the calls of Eastern kingbirds, Western kingbirds, and Western meadowlarks (*Sturnella neglecta*), a sympatric species that is more distantly related and that does not act as a nest predator, I hope to assess difference in response to conspecific and heterospecific challengers. If conspecific challengers represent a greater potential threat through competition for resources or paternity than the threat posed by heterospecific challengers, a higher intensity of aggression would be expected in response to conspecific calls. Given the divergence in nest site preference between Eastern and Western kingbirds, and the prevalence of extrapair fertilizations, I would expect the greatest intensity of aggression to occur in response to conspecific challengers, followed by heterospecific kingbird challengers, and the least intensity of aggression to occur in response to Western meadowlarks, which overlap less in terms of ecological requirements with either kingbird species than they do with each other.

Methods

This study was conducted at the National Bison Range in Charlo, MT, USA (47°33'N, -114°22'W) and on nearby private land between June 26th and July 28th, 2018. Surveys were performed between 6 and 11 AM (Tsipoura and Allen 2013). Eastern (*Tyrannus tyrannus*) and Western kingbirds (*Tyrannus verticalis*) were identified visually and by call. Bison range grasslands, and areas of mixed-grassland with trees and access to streams were of primary interest due to kingbird feeding and nesting preferences (Bergin 1992, Murphy 2001, Murphy 2007). Because subjects were not banded, and thus could not be distinguished individually, new individuals of the same species were only recorded if they were at least 50 m from the last recorded individual (unless individuals were seen at the same time and confirmed to be distinct) to reduce risk of pseudoreplication (Henger and Hauber 2014). A total of 71 Eastern and 35 Western kingbirds were recorded over the course of 21 surveys.

Behavior trials were not performed within 20 m of nest sites to minimize potential reproductive disruption. When kingbirds were located a suitable distance from a nest, the calls of either an Eastern kingbird, Western kingbird, or Western meadowlark were presented. Presentation of calls was approved by the University of Notre Dame IACUC (Protocol number 17-04-3820). Calls were obtained from the xeno-canto database, and were presented using an Anker A3143 speaker (Anker Technology Co. Limited, Reading, UK) at maximum volume placed 10-15 m from the subject bird. 8 different recordings of each type (Eastern and Western kingbird, Western meadowlark) were obtained, and applied in random order to decrease risk of pseudoreplication (Yasukawa et al. 2016). During each trial, vocalizations were played for 5-minute intervals. Recordings of less than 5 min were looped.

Behaviors were recorded using zero-one scan sampling every 15 s during the 5 min playback period, for a total of 20 sampling intervals. Observation continued for a full 5 min even if the

subject bird flew away. Behaviors of interest were determined based on previous playback experiments (Henger and Hauber 2014, Yasukawa et al. 2016), as well as species-specific behavioral studies (Smith and Smith 1992), and behaviors catalogued in *The Birds of North America* (Gamble and Bergin 1996, Murphy and Pyle 2018) (see Table 1). Thirty-six presentations (12 conspecific, 12 Western kingbird, and 12 Western meadowlark) were made to Eastern kingbirds, and 19 presentations (6 conspecific, 7 Eastern kingbird, and 6 Western meadowlark) were made to Western kingbirds.

Data analysis

All analyses were conducted using RStudio Desktop version 1.1.456 (R Development Core Team 2018). Principle components analyses (PCAs) were performed using proportional data from the behavioral trials in order to establish a composite measure of aggression from the behaviors scored. A PCA of both Eastern and Western kingbird trials was performed using a net score of all vocalizations rather than species-specific vocalizations that might obscure other trends. Further PCAs were calculated for Eastern and Western kingbird trials separately, with species-specific behaviors included. A 2-factor ANOVA was performed with PC1 scores as the response variable and respondent and challenger species as factors. 1-factor ANOVAs were performed with the species-specific PC1 scores to assess whether Eastern or Western kingbird species-specific responses varied depending on the call presented.

Further ANOVAs were conducted with single behavior response variables to present a more detailed picture of behavioral variation. Arcsine square root transformations were applied to normalize these data. P-values of less than 0.05 were considered significant. Post-hoc Tukey HSD analyses were conducted for significant comparisons.

Results

Principle Components Analyses

PCA performed on a correlation matrix of Eastern and Western kingbird behavioral responses produced no eigenvectors with eigenvalues greater than 1. Seven components explained 18.8% of total variance. PC1 had an eigenvalue of 0.076, explained 40.7% of inertia, and was characterized by high positive loadings for percent of intervals in which the subject faced the speaker, and high negative loadings for percent of intervals in which the subject vocalized. PC2 had an eigenvalue of 0.035, explained 18.6% of inertia, and was characterized by high positive loadings for percent of intervals in which the subject approached or flew over the speaker, and high negative loadings for facing the speaker and vocalizing.

PCA performed on a correlation matrix of Eastern kingbird behavioral responses produced no eigenvectors with eigenvalues greater than 1. Nine components explained 29.0% of total variance. PC1 had an eigenvalue of 0.097, explained 33.5% of inertia, and was characterized by high percent of intervals facing the speaker, and low percent of intervals vocalizing. PC2 had an eigenvalue of 0.057, explained 19.7% of inertia and was characterized by a relatively high percent of intervals producing “*Dzeer*” vocalizations, and a low percent of intervals producing “*Pi-teer*” vocalizations, flying over the speaker, and approaching the speaker. PCA performed on a correlation matrix of Western kingbird behavioral responses produced no eigenvectors with eigenvalues greater than 1. Eight components explained 21.3% of total variance. PC1 had an eigenvalue of 0.096, explained 44.9% of inertia, and was characterized by high percent of intervals producing “*Kee-kee*” vocalizations, and a relatively low percent of intervals facing the speaker. PC2 had an eigenvalue of 0.037, explained 17.5% of inertia, and was characterized by a relatively high percent of intervals producing “*pwuh-T*” or “*Kee-kee*” vocalizations, producing buzz calls, and flying over the speaker, and a low percent of intervals facing the speaker.

PC1 scores were not found to vary by respondent or challenger species based on two-factor ANOVA results (see Fig. 1). PC1 scores from the Eastern and Western kingbird specific PCAs did not vary by species of challenger based on one-factor ANOVA results.

Analysis of single response variables

Eastern kingbirds approached and flew over the speaker more frequently than did Western kingbirds, but frequency of other scored behaviors were numerically similar (see Fig. 2). Two-factor ANOVAs were performed to assess the effect of respondent and challenger species on single response variables. Arcsine square root transformations were applied to proportions of intervals in which a behavior was performed to normalize distributions. Neither respondent nor challenger species were found to affect the proportion of intervals in which the respondent produced vocalizations, fluttered their wings, or approached or flew over the speaker.

Challenger species, but not respondent species, was found to affect the proportion of intervals in which the respondent faced the speaker ($F_{2,55} = 5.73$, $P = 0.0059$) (see Fig. 2). Post-hoc analyses indicated that respondents spent more time facing the speaker when either Eastern ($P = 0.0077$) or Western kingbird ($P = 0.024$) calls were played than when Western meadowlark calls were played, but that time spent facing the speaker did not vary when Eastern and Western kingbird challenger trials were compared ($P = 0.91$).

Eastern kingbirds responded with the higher frequency of scored behaviors to conspecific calls; this was the case for facing, approaching, and flying over the speaker, fluttering their wings, and net vocalizations (see Fig. 2). They produced “*Pi-teer*,” “*Dzeer*,” and kitter call vocalizations at the highest frequency in response to conspecific calls, with Western kingbird calls leading to almost as high a frequency of kitter calls (see Fig. 3). Western kingbird calls elicited a higher frequency of scored behaviors than meadowlark calls, except in the cases of net

vocalizations and “*Dzeer*” vocalizations (see Fig. 2-3). One-factor ANOVAs were performed to assess whether Eastern kingbird respondents varied species-specific behaviors depending on the challenger call presented. The proportion of intervals in which “*Dzeer*,” “*Pi-teer*,” and kitter-call vocalizations were produced did not vary with challenger species. The proportion of intervals in which Eastern kingbirds faced the speaker did vary with challenger species ($F_{2,36} = 5.52$, $P = 0.0089$). Post-hoc analyses indicated that respondents spent more time facing the speaker when Eastern kingbird calls were played than when Western meadowlark calls were played ($P = 0.0066$), but that time spent facing the speaker did not vary when Eastern and Western kingbird ($P = 0.43$) or Western kingbird and Western meadowlark ($P = 0.11$) calls were compared.

Western kingbirds did not vary their frequency of facing or approaching the speaker, or producing vocalizations much between responding to Eastern and Western kingbird calls (see Fig. 2). However, their frequency of scored behaviors was generally higher in response to both con- and heterospecific kingbirds than to Western meadowlarks. “*Kee-kee*” and buzz call vocalizations were produced more frequently in response to Eastern kingbird calls; “*Kee-kee*” vocalizations did not vary much in frequency between conspecific and Western meadowlark calls, while buzz calls were not produced at all during meadowlark trials (see Fig. 4). “*Pwuh-T*” vocalizations were produced more frequently in response to conspecific calls. One-factor ANOVAs were performed to assess whether Western kingbird respondents varied species-specific behaviors depending on the challenger call presented. No variation in behavioral responses were detected among species of challengers.

Discussion

Eastern kingbirds exhibited the highest frequency of most scored behaviors in response to conspecific calls, supporting the hypothesis that intraspecific competition may be more

ecologically important in this population than heterospecific competition with Western kingbirds. Western kingbirds exhibited similar frequencies of scored behaviors in response to conspecific and Eastern kingbird calls, both of which tended to elicit greater aggression than Western meadowlark calls. Western kingbirds responded as or more aggressively to Eastern kingbird challengers as to conspecific ones, which may indicate that interspecific competition is relatively more important to this population than it is to the more abundant Eastern kingbird. While differences were observable at a count level, most were not supported by statistical testing. At least, recognition of heterospecific kingbird calls relative to non-kingbirds is supported by the higher frequency at which kingbirds faced the speaker in response to kingbird calls compared to meadowlark calls, though this alone is not strong statistical support for higher overall aggression. Inability to include sex as a factor or perform repeated trials with banded individuals may limit how much behavioral variance can be explained.

The responses of Eastern kingbirds generally support a greater magnitude of aggression toward conspecific individuals than heterospecific ones. The production of “*Pi-teer*,” “*Dzeer*,” and kitter call vocalizations in response to conspecific calls is consistent with unstable or agitated interactions, territory defense, and intruder encounters (Smith and Smith 1992, Murphy and Pyle 2018). Western kingbird calls elicited these responses at a higher frequency than did meadowlark calls, and elicited kitter calls at close to the same frequency as conspecific calls. Eastern kingbird responses showed a fairly high degree of variation, often to a greater degree than Western kingbirds (see Fig. 1-2). High variability has been observed in other populations during studies of nest defense (Redmond 2015). Individual behavioral variation may make it difficult to use interspecific aggression as a proxy for interspecific competition, though it may have important consequences for the distribution of Eastern kingbirds within a habitat, the structure of the

population, and the degree of both inter- and intraspecific competition that occurs (Bolnick et al. 2003).

Western kingbirds appeared to differentiate less between conspecific and heterospecific kingbird challengers in terms of overall responsiveness (see Fig. 2). However, the specific vocalizations produced do seem to diverge between challenger types: “*Kee-kee*” and buzz call vocalizations were produced at a greater frequency in response to Eastern kingbird calls, followed by conspecific calls, and were more infrequent in response to meadowlark calls (see Fig. 4). “*Kee-kee*” vocalizations may be associated with agitation, while buzz calls are typically produced in response to predators or conspecific challengers, usually by males (though this was not the case in this population) (Gamble and Bergin 1996). Buzz calls were not produced at all in response to meadowlarks, which is consistent with the association between this behavior and aggression toward a threat or competitor. “*Pwuh-T*” vocalizations were produced most frequently in response to conspecific challengers, followed by Eastern kingbirds (see Fig. 4). This vocalization is usually associated with territoriality, and is more commonly produced by males (Gamble and Bergin 1996).

Limitations

Because birds were not banded, my ability to determine the sex of respondents, or reliably perform multiple trials with the same respondent to assess variation in individual behavior was inhibited. Aggressive behaviors typically differ between kingbird sexes: male nest defense tends to increase during the nestling stage, while female nest defense does not tend to vary much over time; females provision nestlings at twice the rate of males, and may thus have less energy to invest in interference competition or other forms of aggression (Redmond et al. 2009). Furthermore, females do not risk losing nest maternity to extrapair fertilizations, and thus may

not share the motivation of intrasexual competition that is present for males in the nest patch area (Redmond 2015). Thus, sexual differences in behavior may explain some of the unexplained variation in behavior, or may be masking effects of respondent and challenger identity.

Presentation of challenger calls without the added visual stimulus of a mount may have reduced the magnitude and variety of aggressive responses. No instances of respondents swooping at or touching the speaker, or presenting wing whir or crown patch displays were observed. During surveys, multiple aggressive interactions that included physical contact or chasing were observed between kingbirds and other birds in the vicinity: Eastern kingbirds chased Western meadowlarks, barn swallows (*Hirundo rustica*), brown-headed cowbirds (*Molothrus ater*), Brewer's blackbirds (*Euphagus cyanocephalus*), Western kingbirds, and, most frequently, other Eastern kingbirds; Western kingbirds chased common starlings (*Sturnus vulgaris*), Eastern kingbirds, and other Western meadowlarks with intraspecific aggression again being most common. In a field setting with stimulus from other birds competing for attention, the addition of a mount to challenger calls may produced stronger responses. Finally, adding a treatment with a silent speaker would help to differentiate between baseline behaviors of respondents and responses to playback calls.

Future Works

Performing similar behavioral trials with allopatric populations may also provide a useful comparison that could establish the degree to which exposure to heterospecific kingbirds affects magnitude of aggression. Adding a treatment with a nest predator call could allow comparison of the role of predation and that of competition in kingbirds' characteristic aggression.

Determining the degree of habitat separation between Eastern and Western kingbirds at the National Bison Range, as well as assessing other aspects of ecological overlap such as diet

composition and perch use may help to explain some variation in aggressive responses by establishing the degree of interspecific competition that would be expected. Comparing rates of nest depredation between species may also clarify whether differing nest site use results from differing ecological requirements or a weaker competitor being pushed into less desirable locations by a dominant species.

Acknowledgements

I would like to thank the Bernard J. Hank Family Endowment for providing project funding, and the University of Notre Dame's Environmental Research Center for facilitating this research. Thanks also to the National Bison Range and Confederated Salish and Kootenai tribes for permitting data collection at the bison range. David Flagel deserves recognition for providing research materials, feedback on drafts, and advice about statistical analyses. Katherine Bailey also gave critical guidance for completing analyses. Particular thanks to Ken Yasukawa for guidance in developing the study design and methodology. Finally, I would like to thank Erin Nguyen, Celia Montemurri, and Daniel De Jesús for assisting with data collection.

References

- Bergin, T. M. (1992). Habitat Selection by the Western Kingbird in Western Nebraska: A Hierarchical Analysis. *The Condor* 94:903–911.
- Bolnick, D. I., R. Svanback, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister (2003). The Ecology of Individuals: Incidence and Implications of Individual Specialization. *The American Naturalist* 161:1–28.
- Carrete, M., J. A. Sanchez-Zapata, J. L. Tella, J. M. Gil-Sanchez, and M. Moleon (2006). Components of breeding performance in two competing species: habitat heterogeneity, individual quality and density-dependence. *Oikos* 112:680–690.
- Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case (2002). The interaction between predation and competition: a review and synthesis. *Ecology Letters* 5.

- Cotton, P. A. (2008). Temporal partitioning of a floral resource by territorial hummingbirds. *Ibis* 140.
- Dolan, A. C., M. T. Murphy, L. J. Redmond, K. Sexton, and D. Duffield (2007). Extrapair paternity and the opportunity for sexual selection in a socially monogamous passerine. *Behavioral Ecology* 18:985–993.
- Gamble, L. R., and T. M. Bergin (1996). Western Kingbird (*Tyrannus verticalis*). In *The Birds of North America*. The Birds of North America, Inc., Philadelphia, PA.
- Henger, C. S., and M. E. Hauber (2014). Variation in antiparasitic behaviors of Red-winged Blackbirds in response to simulated Brown-headed Cowbirds. *The Wilson Journal of Ornithology* 126:488–499.
- Jankowski, J. E., S. K. Robinson, and D. J. Levey (2010). Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. *Ecology* 91.
- MacKenzie, D. I. (1979). Nest site selection and coexistence in eastern and western kingbirds at Delta Marsh, Manitoba. [Online.] Available at <https://mspace.lib.umanitoba.ca/handle/1993/6321>.
- MacKenzie, D. I., and S. G. Sealy (1981). Nest site selection in Eastern and Western Kingbirds: a multivariate approach. *The Condor* 83:310–321.
- Maher, C. R. (2000). A Review of Ecological Determinants of Territoriality within Vertebrate Species. *The American Midland Naturalist* 143:1–29.
- Markova, A., and Serebryakov (2016). Differences in aggressive behavior of related species of flycatchers (*Muscicapidae*) family. *Biology* 72:63–69.
- Murphy, M. T. (1983). Nest Success and Nesting Habits of Eastern Kingbirds and Other Flycatchers. *The Condor* 85:208–219.
- Murphy, M. T. (2001). HABITAT-SPECIFIC DEMOGRAPHY OF A LONG-DISTANCE, NEOTROPICAL MIGRANT BIRD, THE EASTERN KINGBIRD. *Ecology* 82.
- Murphy, M. T. (2007). LIFETIME REPRODUCTIVE SUCCESS OF FEMALE EASTERN KINGBIRDS (*TYRANNUS TYRANNUS*): INFLUENCE OF LIFESPAN, NEST PREDATION, AND BODY SIZE. *The Auk* 124:1010–1022.
- Murphy, M. T., C. L. Cummings, and M. S. Palmer (1997). Comparative Analysis of Habitat Selection, Nest Site and Nest Success by Cedar Waxwings (*Bombycilla cedrorum*) and Eastern Kingbirds (*Tyrannus tyrannus*). *The American Midland Naturalist* 138:344–356.
- Murphy, M. T., and P. Pyle (2018). Eastern Kingbird (*Tyrannus tyrannus*): Sounds and vocal behavior. Cornell Lab of Ornithology.

- Qvanstrom, A., N. Svedin, C. Wiley, T. Veen, and L. Gustafsson (2005). Cross-fostering reveals seasonal changes in the relative fitness of two competing species of flycatchers. *Biology Letters* 1.
- Redmond, L. J. (2015). The Biology of Eastern Kingbirds at Malheur National Wildlife Refuge: Survival, Reproduction, and Testosterone Secretion. [Online.] Available at https://pdxscholar.library.pdx.edu/cgi/viewcontent.cgi?referer=https://www.google.com/&httpsredir=1&article=3627&context=open_access_etds.
- Redmond, L. J., M. T. Murphy, A. C. Dolan, and K. Sexton (2009). Parental Investment Theory and Nest Defense by Eastern Kingbirds. *The Wilson Journal of Ornithology* 121:1–11.
- Rohwer, S. A. (1973). SIGNIFICANCE OF SYMPATRY TO BEHAVIOR AND EVOLUTION OF GREAT PLAINS MEADOWLARKS. *International Journal of Organic Evolution* 27:44–57.
- Saetre, G.-P., E. Post, and M. Kral (1999). Can Environmental Fluctuation Prevent Competitive Exclusion in Sympatric Flycatchers? *Proceedings: Biological Sciences* 266:1247–1251.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier (1985). Predation, Competition, and Prey Communities: A Review of Field Experiments. *Annual Review of Ecology and Systematics* 16:269–311.
- Smith, W. J., and A. M. Smith (1992). Behavioral Information Provided By Two Song Forms of the Eastern Kingbird, *Tyrannus*. *Behaviour* 120:90–102.
- Tsipoura, N., and M. Allen (2013). 2013 LOWER RARITAN BIRD SURVEY PROTOCOL. Audubon Society.
- Vallin, N., A. M. Rice, H. Arnsten, K. Kulma, and A. Qvanstrom (2012). Combined effects of interspecific competition and hybridization impede local coexistence of *Ficedula* flycatchers. *Evolutionary Ecology* 26:927–942.
- Verbeek, N. A. M. (1975). Comparative Feeding Behavior of Three Coexisting Tyrannid Flycatchers. *The Wilson Bulletin* 87:231–240.
- Welden, C. W., and W. L. Slauson (1986). The Intensity of Competition Versus its Importance: An Overlooked Distinction and Some Implications. *The Quarterly Review of Biology* 61:23–44.
- Yasukawa, K., J. Lindsey-Robbins, C. S. Henger, and M. E. Hauber (2016). Antiparasitic behaviors of red-winged blackbirds (*Agelaius phoeniceus*) in response to simulated brown-headed cowbirds (*Molothrus ater*): further tests of the frontloaded parasite-defense hypothesis. *The Wilson Journal of Ornithology* 128:475–690.

Table I

Behavior	Species	Source
Faces speaker	Both	Henger and Hauber 2014
Approaches speaker	Both	Henger and Hauber 2014
Flies over speaker	Both	Henger and Hauber 2014
Swoops at speaker	Both	Henger and Hauber 2014
Makes contact with speaker	Both	Henger and Hauber 2014
Extends head with legs bent and tail spread (crouch)	Both	Gamble and Bergin 1996
Partial extension of wings followed by rapid fluttering (wing flutter)	Both	Gamble and Bergin 1996
Sudden movement of wings producing a whirring sound (wing whir display)	Both (males only)	Gamble and Bergin 1996
Opens and closes bill, producing snapping sound (bill snap)	Both	Gamble and Bergin 1996
<i>Pi-teer</i> vocalization	Eastern	Murphy and Pyle 2018
<i>Dzeer/ T-zee</i> vocalization	Eastern	Smith and Smith 1992, Murphy and Pyle 2018
Kitter-call (chatter-zeer)	Eastern	Smith and Smith 1992, Murphy and Pyle 2018
Raises orange/red crown feathers (crown patch reveal)	Western	Gamble and Bergin 1996
<i>Kee-kee</i> vocalization	Western	Gamble and Bergin 1996
<i>Pwuh-T</i> vocalization	Western	Gamble and Bergin 1996
Buzz call	Western (typical of males)	Gamble and Bergin 1996

Figure Legends

Fig. 1 Variation in PC1 scores between Eastern and Western kingbirds. Eastern kingbirds exhibit a greater range of scores, particularly in response to Western meadowlark calls. Western kingbirds show less variation, with scores skewing negative. PC1 scores are positively associated with intervals spent facing the speaker, and negatively associated with vocalizations.

Fig. 2 Proportion of intervals in which the respondent **A)** faced the speaker, **B)** approached the speaker, and **C)** produced vocalizations, the three most frequently occurring behavior categories. Eastern kingbirds exhibit the highest mean frequency of responses to conspecific calls, followed by Western kingbird and then Western meadowlark calls. Western kingbirds exhibit higher mean frequency of responses to kingbird than meadowlark calls, but there is less differentiation between con- and heterospecific kingbird challengers.

Fig. 3 Proportion of intervals in which Eastern kingbirds produced **A)** *Pi-teer*, **B)** *Dzeer*, or **C)** kitter call vocalizations in response to different challenger species. *Pi-teer* and kitter call vocalizations occurred most frequently when conspecific calls were played, followed by Western kingbird and then Western meadowlark calls. *Dzeer* vocalizations occurred most frequently when conspecific calls were played, followed by meadowlark calls.

Fig. 4 Proportion of intervals in which Western kingbirds produced **A)** *Kee-kee*, **B)** *Pwuh-T* or **C)** buzz call vocalizations in response to different challenger species. *Kee-kee* vocalizations occurred most frequently when Eastern kingbird calls were played, followed by conspecific calls and then meadowlark calls. Kitter calls occurred with about the same frequency in response to Eastern and Western kingbird calls. *Pwuh-T* vocalizations occurred most frequently when conspecific calls were played, followed by Eastern calls and then meadowlark calls.

Fig. 1

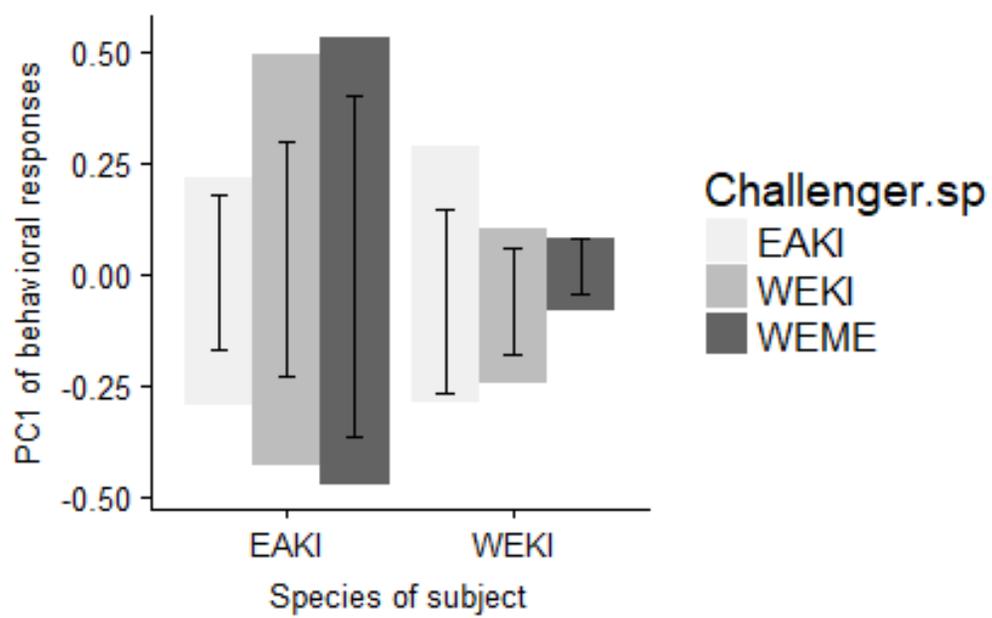
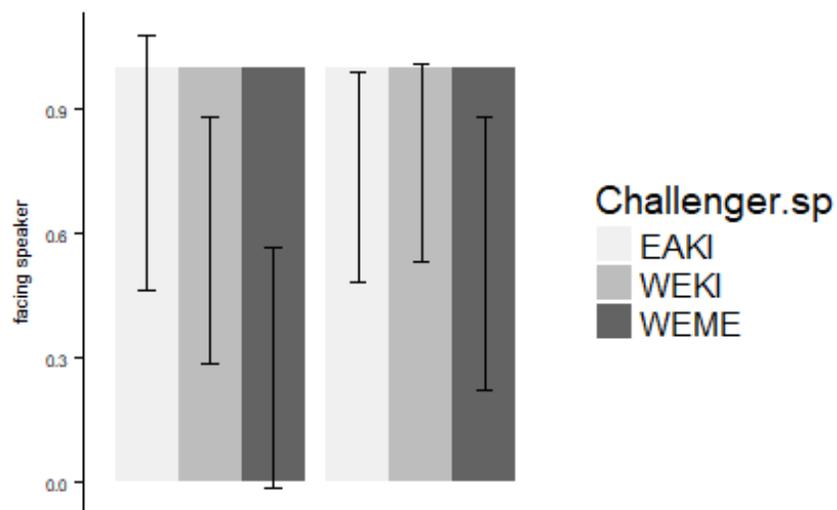
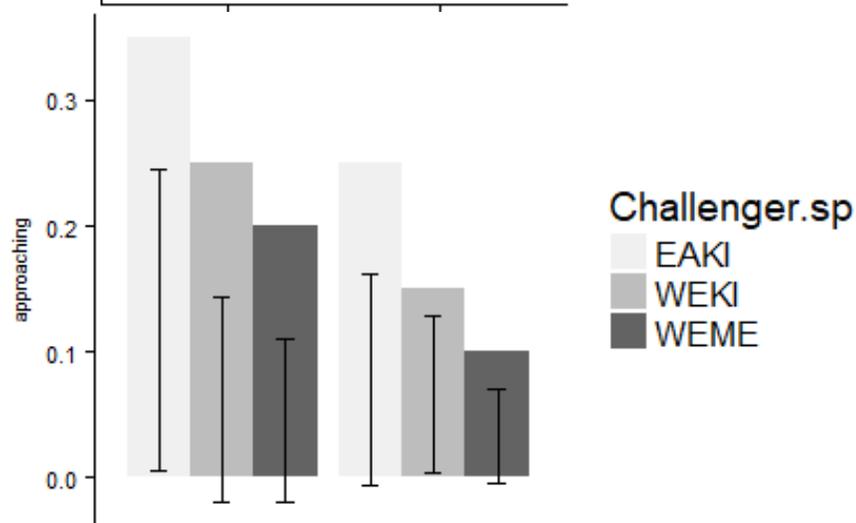


Fig. 2

A)



B)



C)

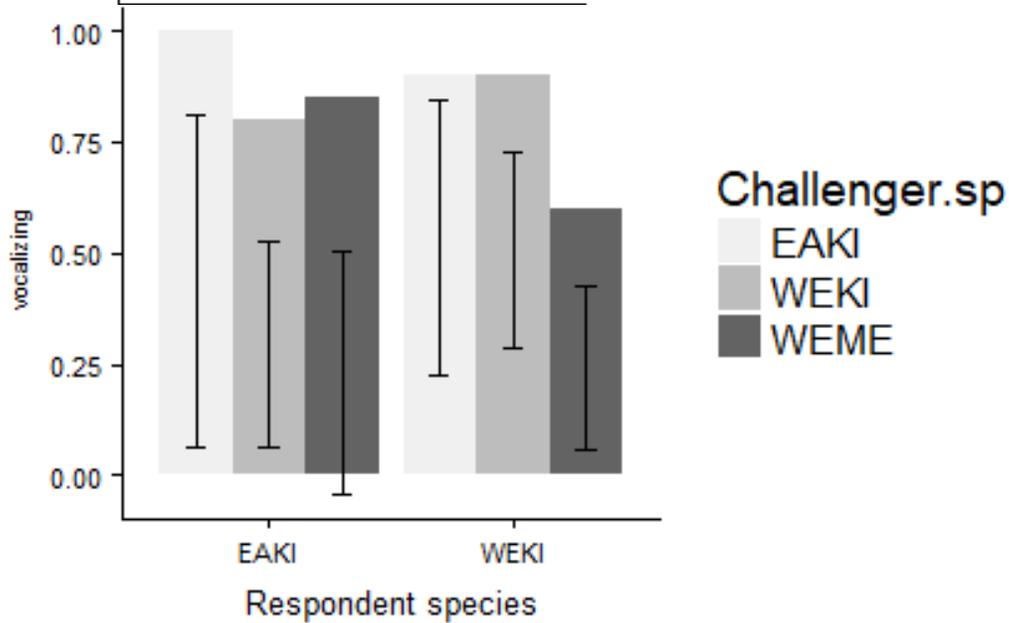
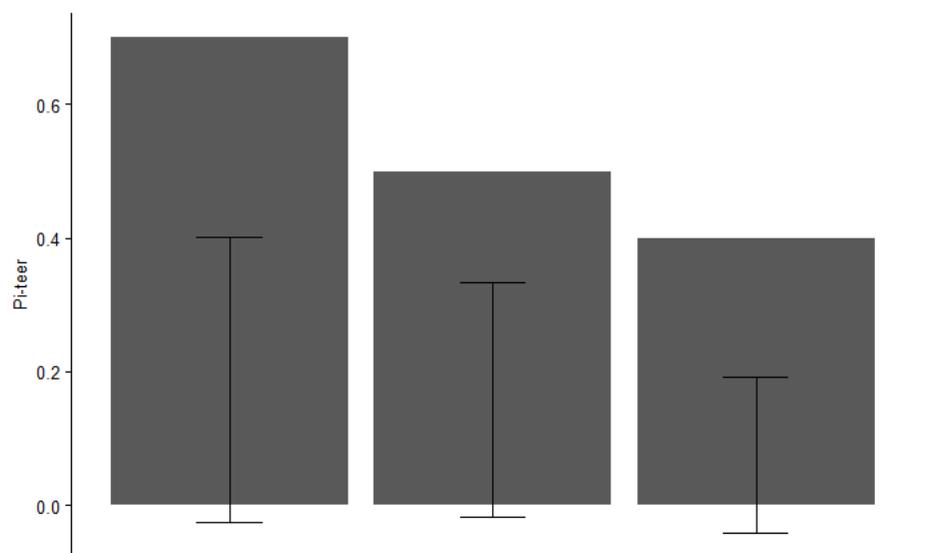
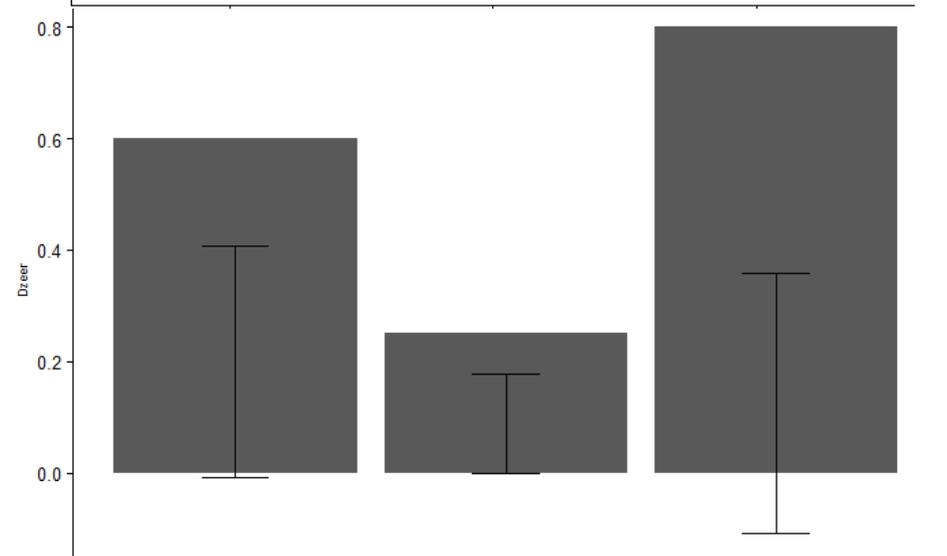


Fig. 3

A)



B)



C)

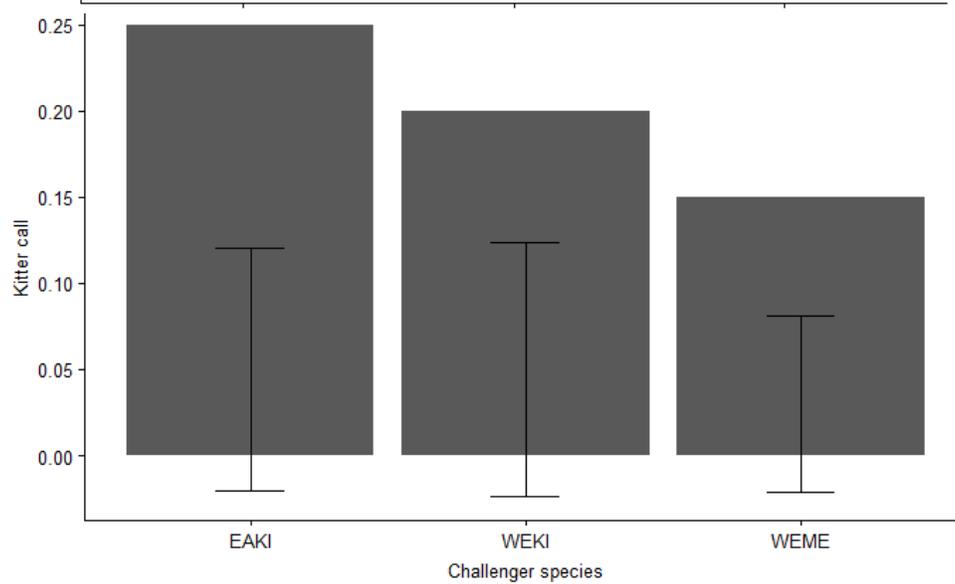


Fig. 4

