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VOCALIZATIONS OF ADULT AMERICAN KESTRELS (*FALCO SPARVERIUS*):
EFFECT OF BREEDING STAGE, SEX, AND CONTEXT ON CALL USE AND
CHARACTERISTICS

BY

MARK ADAM WINLAND

THESIS APPROVED:



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CHARACTERISTICS

BY

MARK ADAM WINLAND

Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

2019

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DEDICATION

I dedicate this thesis to my wonderful wife Courtney who has encouraged me and helped me get through the bad times, and to my parents whose support is what allowed me to pursue this endeavor.

ACKNOWLEDGMENTS

Thank you to my advisor, committee members, instructors, and fellow students for the assistance, encouragement, and opportunities for growth each of you have provided me.

ABSTRACT

American Kestrels (*Falco sparverius*) are small falcons with a vocal repertoire known to consist of three different vocalizations: whine, chitter, and klee calls. However, the characteristics and contextual use of these calls have not been quantified. To determine the characteristics of these calls and better understand possible functions, I conducted a combined observational and experimental study of American Kestrels in Madison County, Kentucky, from February to July 2013. I observed kestrels and recorded all vocalizations uttered by males and females during different breeding stages and different behavioral contexts. In addition, I conducted playback experiments using the whine, chitter, and klee calls, and presentation experiments with models (study skins) of conspecifics and potential nest predators (human). I found that the characteristics of vocalizations of males and females were similar, but the chitter calls of males were at a higher frequency than those of females. Sex and call context had significant effects on the use of calls and number of calls per bout, with klee calls used significantly more often and with more calls per bout during heterospecific contexts than during either close or distant intersexual interactions. Whine calls were used more during close and distant intersexual interactions than during heterospecific interactions. All chitter calls uttered by males and females were in either close or distant intersexual contexts. Use of klee calls during encounters with other species near nests, particularly humans and Red-tailed Hawks (*Buteo jamaicensis*), suggests that they serve an aggressive function. Whine calls appear to be important for communication among male, female, and fledgling American Kestrels and appear to serve in soliciting the approach of a mate or, for fledglings, an adult. Chitter calls appear to play a role in pair

formation and communication between mates before and after females begin incubating eggs, possibly informing mates of their approach or, as with whine calls, soliciting the approach of a mate. Analysis of how American Kestrels use and vary the characteristics of calls based on sex, behavioral context, and breeding stage improves our understanding of their function and how kestrels might vary call characteristics to convey information to conspecifics.

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I. Introduction

Most studies of the structure and function of avian vocalizations have focused on passerines, with less known about the vocal behavior of diurnal birds of prey (Sánchez 2007). Studies of raptor vocalizations have primarily been descriptive and qualitative, often with just verbal descriptions of calls or, at best, representative sonograms plus an explanation of possible functions. For example, Rosenfield and Bielefeld (1991) examined the vocal behavior of Cooper's Hawks (*Accipiter cooperii*) during the pre-incubation phase of breeding, describing four different vocalizations and suggesting possible functions. Farquhar (1993) reported individual and intersexual variation in the calls of White-tailed Hawks (*Buteo albicaudatus*), and Carlier (1995) described two calls and the contexts in which they were used by Peregrine Falcons (*Falco peregrines*). Other investigators have provided general information about the vocalizations of Ospreys (*Pandion haliaetus*; Bretagnolle and Thibault 1993), Lanner Falcons (*Falco biarmicus*; Leonardi et al. 2012), Northern Goshawks (*Accipiter gentilis*; Penteriani 2001, Penteriani et al. 2002), and several species of Australian falcons and kites (Jurisevic 1998).

The vocalizations of non-passerines, including raptors (Jurisevic 1998), are generally considered simpler and more stereotyped than those of passerines (e.g., Popp and Ficken 1991, Naugler and Smith 1992, Williams and Houtman 2008). However, recent studies indicate that some non-passerines vary the characteristics of calls to convey information to conspecifics. For example, male Common Loons (*Gavia immer*) increase the duration of their territorial yodel calls to communicate greater aggressive motivation (Mager et al. 2012). Other non-oscines reported to vary the characteristics of

calls to convey information concerning motivation or individual quality include Pigeon Guillemots (*Cephus columba*; Nelson 1984) and Hoopoes (*Upupa epops*; Martin-Vivaldi et al. 2004). In addition, Wilson and Evans (2012) found that Domestic Chickens (*Gallus gallus domesticus*) communicate the perceived size, speed, and distance from avian predators to conspecifics by varying the characteristics of their alarm calls.

Previous studies have provided limited information about the vocal behavior of raptors and, even where general descriptions of vocal repertoires have been provided, little quantitative information is available concerning the contextual use of different calls. No one to date has examined how raptors might vary the characteristics of their calls to convey information to conspecifics. Therefore, additional study is needed to improve our understanding of the characteristics and functions of the vocalizations of raptors, and to determine if raptors, as reported for some other non-oscines, vary the characteristics of calls to convey more precise information (e.g., concerning motivation or degree of threat posed by predators) to conspecifics.

Few investigators have examined the vocal behavior of American Kestrels (*Falco sparverius*), small, cavity-nesting falcons found throughout much of the western hemisphere (Smallwood and Bird 2002). Willoughby and Cade (1964) described three distinct vocalizations referred to as the whine, chitter, and klee (or killy) calls (Figure 1), and noted the general contexts in which these calls were uttered. In a study of captive kestrels, Mueller (1971) also described the general contexts in which these calls were given, and noted the use of combination calls such as whine-chitter and klee-

chitter calls. However, neither the characteristics of, nor contextual use of these calls has been quantified.

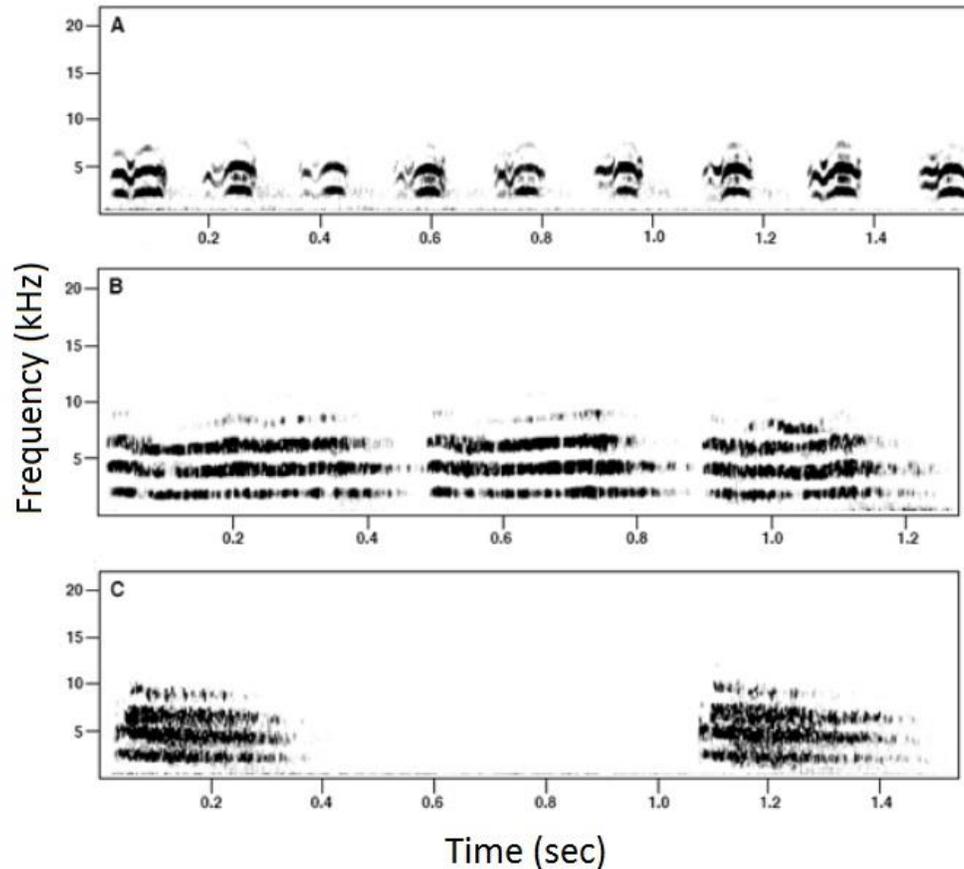


Figure 1. Sonograms of the vocalizations of American Kestrels. (A) klee call, (B) whine call, and (C) chitter call (Figure modified from Smallwood and Bird 2002).

The characteristics of the three primary calls of American Kestrels are known to vary. Smallwood and Bird (2002) noted that (1) the klee call consisted of a variable number of notes (generally 3 to 6) and is often given during interactions with conspecifics and heterospecifics, (2) the whine call varies in duration and is given during courtship, and (3) chitter calls can vary in duration. The ability of kestrels to

vary the characteristics of these calls suggests that, by doing so, they may be conveying different information to conspecifics.

Although previous investigators have provided general information about the vocal behavior of American Kestrels, additional study is clearly needed. Thus, my objectives were to (1) quantify the characteristics and contextual use of the calls of American Kestrels, and (2) determine if kestrels vary the characteristics of calls to convey information to conspecifics and heterospecifics.

II. Methods

My study was conducted at the Blue Grass Army Depot, Central Kentucky Wildlife Management Area, and Eastern Kentucky University in Madison County, Kentucky. Nest boxes (N = 20) were placed in areas with suitable habitat during December 2012 and January 2013 to attract breeding pairs.

Observations

From 15 March to 31 July 2013, I observed each member of each pair of kestrels (N = 15) during observation periods of ~45-60-min at least twice a week. In addition, nest boxes were checked at least weekly to determine nesting stage (pre-nesting, egg laying, incubation, nestling, and post-fledging). At the beginning of each observation period, I noted on an audio recorder the identity, based on proximity to nest, of the focal pair, date, and breeding stage. During observation periods, I recorded all vocalizations uttered by the focal male and female using a recorder (TCM-59V, Sony, Tokyo, Japan) and a directional microphone (ME-88, Sennheiser, Old Lyme, CT). For each vocalization or bout (i.e., number of calls given each time a kestrel was observed during a particular context where calls appeared to be interrelated), I noted the behavioral context, with contexts categorized as (1) spontaneous calling (not appearing to be interacting with a conspecific or responding to another stimulus such as a potential predator), (2) close intersexual interaction (a mate or other conspecific of the opposite sex within 5 m), (3) distant intersexual interaction (a mate or other conspecific of the opposite sex > 5 m away), (4) close intrasexual interaction (e.g., responding to territorial intrusion by a conspecific of the same sex and approaching within 10 m), (5) distant intrasexual interaction (not approaching within 10 m of a conspecific of the

same sex), and (6) heterospecific interaction (e.g., responding to a potential predator, including predators capable of killing an adult such as a Red-tailed Hawk (*Buteo jamaicensis*) as well as potential nest predators).

Playback Experiments

I also conducted playback experiments to further clarify the possible functions of kestrel vocalizations. Playback experiments were conducted with klee, chitter, and whine calls. Playback tapes were made using recordings obtained from the Macaulay Library of Natural Sounds (Cornell Lab of Ornithology, Ithaca, NY). To avoid pseudoreplication, I made multiple playback tapes for each call type (N = 4) and randomly selected tapes to use for each playback experiment.

One playback experiment with each type of call was conducted in the territory of each pair of kestrels (N = 13 pairs). Experiments were conducted during the pre-nesting (N = 4), incubation (N = 14), and nestling (N = 18) periods. Prior to initiating playback experiments, I placed a speaker (SME-AFS, Saul Mineroff Electronics, Elmont, NY) on a 1-m-high box located ~5 m from the focal pair's nest box. After putting the speaker in place, I moved ~30 – 45 m away, using available vegetation as a 'blind', and waited until I determined the location of both members of the pair and each was at a distance that would ensure they would hear the calls being played (< ~50 m). Each experiment consisted of two 3 min periods: playback and post-playback. During the playback period, calls were broadcast every 10 sec for 3 min at a volume that, to me, was typical for kestrels. During playback, all calls or bouts of calls uttered were recorded and I noted the sex of the calling bird and their distance from the speaker, with distances categorized as close (≤ 5 m) or distant (> 5 m). During a 3-min post-playback

period, I again recorded all calls and noted the sex and distance from the speaker of the vocalizing kestrel.

Conspecific and Predator Presentation Experiments

Presentation experiments were conducted near nest boxes to further clarify the possible functions of kestrel vocalizations and variation in the characteristics of those vocalizations. Four presentation experiments were conducted with each pair of kestrels, including two conspecific presentation experiments, one with a male study skin (N = 14), one with a female study skin (N = 13), and two predator-presentation experiments (N = 8) at each nest during the early-nestling period (7 – 14 days post-hatching) and again during the late-nestling period (15 – 25 days post-hatching).

Conspecific-presentation experiments were conducted during the period prior to and during egg laying. I conducted 12 male and 12 female presentations prior to egg laying and two male and one female presentations during egg laying (one nest was predated before the second female presentation). During these experiments, study skins were mounted to a 2 m pole and placed 4 m in front of the tree or utility pole that focal nest boxes were mounted on. Skins were placed when neither member of the pair was present. I then moved to a position ~30 – 45 m away (again using natural vegetation as a blind) and waited until at least one member of the pair was observed at a location that would allow them to see the study skin. For the next 6 min, I recorded calls and the sex and distance from the study skin of vocalizing kestrels (as described for the playback experiments). After 6 min, I removed the pole and study skin. Successive conspecific-presentation experiments in each territory were at least three days apart.

For the predator-presentation experiments, a human served as the ‘predator.’ For each experiment, the predator stood 20 m from nests (with a ladder) and remained there until at least one member of the pair was in view. The predator then walked to a point below the nest box and remained for 2 min. Next, the predator climbed the ladder to within 1 m of the nest box, remained there for 90 sec, then climbed down the ladder and returned with the ladder to the starting point 20 m from the nest box. After an additional minute, the predator left the area. During each predator-presentation experiment, I stood 30 – 45 m from the nest box and noted all kestrel behaviors and locations (relative to the predator) and recorded all vocalizations. Locations of kestrels to the predator were categorized as very close (≤ 2 m), close (2.1-5 m), or distant (>5 m).

Analysis

All kestrel vocalizations recorded during each observation period and each experiment were analyzed, unless recording quality was too poor to allow accurate analysis. Characteristics of calls measured included duration, number of figures or notes (“a sound which produces a single, complete, and distinct impression uninterrupted by silence greater than two centiseconds”; Shiovitz 1975:133), and frequency at highest amplitude. Recordings were analyzed using sound-analysis software (Raven V1.2.1, Cornell Lab of Ornithology, Ithaca, NY). I used repeated measures analysis of variance to compare the characteristics of calls of male and female kestrels.

To examine the tendency of different calls to be uttered by male and female American Kestrels during different breeding stages, I examined the rates at which

different calls were used by each sex and duration during the different breeding stages (number of calls divided by the duration of observation periods). To examine call use in different contexts, I compared the number of calls per bout (i.e., number of calls given each time a kestrel was observed during a particular context where calls appeared to be interrelated), for males and females in different contexts. Because so few kestrels vocalized during intrasexual interactions (only 19 calls, including 13 klee calls and six whine calls), those contexts (distant intrasexual and close intrasexual) were not included in my analysis; the remaining contexts were close intersexual, distant intersexual, heterospecific and spontaneous. Because multiple observation and recordings were made of each pair of kestrels, I used repeated-measures analysis of variance to (1) compare the rates at which the different calls were uttered by males and females during the different breeding stages, and (2) compare the number of calls given per bout by males and females in different behavioral contexts.

To determine how context might influence the characteristics of the klee, whine, and chitter calls of American Kestrels, I used repeated measures analysis of variance to examine possible differences in number of notes per klee call and the duration of whine and chitter calls of males and female uttered during different breeding stages and in different behavioral contexts. Statistically significant results were followed by post-hoc Tukey's tests to determine which means were significantly different.

All analyses were conducted using the Statistical Analysis System (SAS Institute 2015). Values are presented as means \pm SE.

III. Results

I observed, recorded, and conducted experiments with American Kestrels at 15 nest boxes and recorded vocalizations of birds not associated with nests on two occasions. Mean clutch size of females at these nests was 4.7 ± 0.2 eggs. Young fledged from eight nests (3.3 ± 0.4 young fledging) and four pairs attempted to re-nest after their first clutch was lost. Second nests ($N = 4$) contained an average of four eggs (range = 3-5 eggs), and three of these nests were again lost. A female at the remaining re-nest was still incubating eggs when my study ended (31 July 2013).

Vocalizations

I recorded 3900 calls uttered by 31 American Kestrels, including 2950 klee calls, 833 whine calls, and 117 chitter calls. Overall, klee calls had a mean duration of 1.88 ± 0.02 sec, a mean frequency of 6054 ± 149 Hz, and averaged 10.7 ± 0.1 notes per call. Whine calls had a mean duration of 5.43 ± 0.20 sec and mean frequency of 6046 ± 46 Hz, and chitter calls averaged 2.33 ± 0.39 sec in duration with a mean frequency of 6054 ± 149 Hz.

Klee calls of male and female American Kestrels did not differ in duration ($F_{1,10} = 0.4$, $P = 0.55$), frequency ($F_{1,10} = 0.1$, $P = 0.93$), or number of notes per call ($F_{1,10} = 1.4$, $P = 0.27$). Similarly, characteristics of the whine calls of males and females did not differ (duration: $F_{1,14} = 0.1$, $P = 0.98$; frequency: $F_{1,14} = 0.1$, $P = 0.96$). The chitter calls of males and females did not differ in duration ($F_{1,6} = 1.7$, $P = 0.24$), but did differ in frequency ($F_{1,6} = 6.5$, $P = 0.043$), with the calls of males (6924.6 ± 168.7 Hz) higher in frequency than those of females (4956.0 ± 221.6 Hz).

Effect of Nest Stage and Sex on Call Rate

The rate at which klee calls were given did not differ either between the sexes ($F_{1,19} = 2.7, P = 0.11$) or among nest stages ($F_{3,19} = 1.1, P = 0.37$). In addition, I found no significant interactions between nest stage and sex ($F_{3,19} = 3.5, P = 0.77$). Similarly, I found no difference between either males and females ($F_{1,19} = 0.1, P = 0.72$), among nest stages ($F_{3,19} = 2.1, P = 0.14$), or among the interaction of nest stage and sex ($F_{3,19} = 0.5, P = 0.71$) in the rate at which whine calls were uttered. Too few chitter calls were uttered to allow analysis, but most chitter calls were given during the pre-nesting and incubation periods by both males and females.

Effect of Sex and Context on Use of Calls and Number of Calls per Bout

Use of klee calls by pairs of American Kestrels differed significantly among contexts ($F_{2,18} = 9.8, P = 0.0013$), with more bouts of klee calls ($N = 204$ bouts) during heterospecific contexts (92, 45.1%) than during either close (46, 22.5%) or distant (66, 32.4%) intersexual contexts (Tukey's test, $P < 0.05$). The mean number of klee calls/bout did not differ between the sexes ($F_{1,10} = 0.01, P = 0.95$). However, the difference among contexts in mean number of calls/bout was significant ($F_{2,10} = 5.5, P = 0.0048$), with significantly more calls/bout during heterospecific interactions than during either close or distance intersexual interactions (Tukey's test, $P < 0.05$). I also found a significant interaction between sex and context ($F_{2,3} = 13.8, P = 0.031$), with females uttering significantly more calls/bout than males during heterospecific interactions (Figure 2).

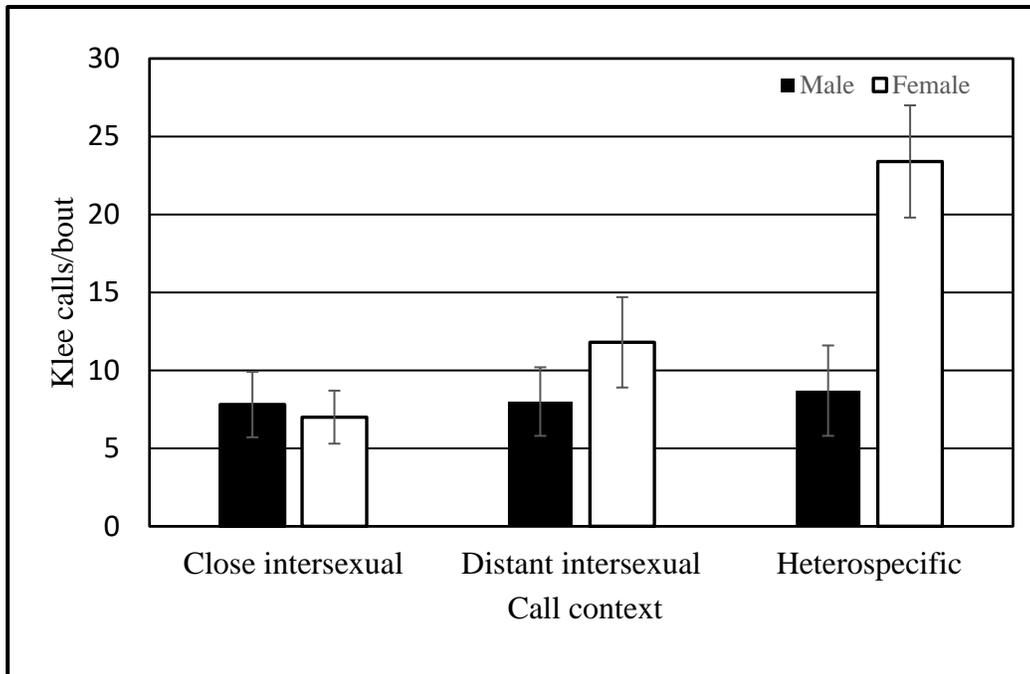


Figure 2. Mean number (\pm SE) of klee calls per bout by male and female American Kestrels during different contexts.

Use of whine calls by pairs of American Kestrels also differed significantly among contexts ($F_{2,33} = 47.0$, $P < 0.001$), with more bouts of whine calls ($N = 207$ bouts) during close (92, or 44.4%) and distant (94, or 46.4%) intersexual contexts than during heterospecific contexts (19, or 9.2%; Tukey's test, $P < 0.05$). For whine calls, I found no difference in the mean number of calls/bout either between the sexes ($F_{1,14} = 1.7$, $P = 0.22$) or among contexts ($F_{2,14} = 2.2$, $P = 0.12$). In addition, I found no significant interaction between sex and context ($F_{2,3} = 0.3$, $P = 0.77$). Too few bouts of chitter calls were recorded to allow analysis, but all bouts of calling by males and females were in either close ($N = 23$) or distant ($N = 13$) intersexual contexts.

Effect of Nest Stage and Context on Call Characteristics

Characteristics of klee calls did not vary among nest stages, including call duration ($F_{3,16} = 0.2$, $P = 0.92$), number of notes per call ($F_{3,16} = 2.0$, $P = 0.16$), and

frequency ($F_{3,16} = 0.8$, $P = 0.54$). Similarly, the duration ($F_{3,14} = 0.8$, $P = 0.54$) and frequency ($F_{3,14} = 2.7$, $P = 0.09$) of whine calls, and the duration ($F_{2,3} = 1.4$, $P = 0.36$) and frequency ($F_{2,3} = 0.2$, $P = 0.84$) of chitter calls did not vary among nest stages.

Characteristics of klee calls did not vary among contexts, including call duration ($F_{4,27} = 0.6$, $P = 0.65$), number of notes per call ($F_{4,27} = 1.2$, $P = 0.37$), and frequency ($F_{4,27} = 1.8$, $P = 0.15$). Similarly, the duration ($F_{4,35} = 1.2$, $P = 0.34$) and frequency ($F_{4,35} = 1.6$, $P = 0.19$) of whine calls were not affected by contexts. Too few bouts of chitter calls were recorded to allow analysis, but nearly all calls (96%) were during close and distant intersexual contexts.

Conspecific Presentations

I conducted presentation experiments with study skins of a male ($N = 14$ nests) and female ($N = 13$ nests) American Kestrels. During 10 of 27 trials (37%), kestrels responded by vocalizing; kestrels were present, but did not vocalize during 17 trials (63%). Overall, kestrels ($N = 10$, 5 males, 4 females, and 1 unknown sex) uttered 100 calls during the 10 6-minute trials, including 69 whine calls (1.3 per minute), 30 chitter calls (0.6 per minute), and one klee call.

During experiments with a study skin of a female American Kestrel, chitter calls were given at mean rates of 0.94 ± 0.24 calls/min by females ($N = 3$) and 0.50 ± 0.10 calls/min by males ($N = 3$). For whine calls, mean calling rates were 0.71 ± 0.34 calls/min for females ($N = 4$) and 1.33 ± 0.26 calls/min for males ($N = 5$). One male also gave a single klee call during presentation of the study skin of the female kestrel.

During experiments with a study skin of a male American Kestrel, one female responded with two chitter calls and another female responded with two whine calls. Three different males responded and uttered 0.39 ± 0.15 whine calls/min.

Predator-Presentation Experiments

During 16 predator-presentation experiments (eight during the early nestling stage and eight during the late nestling stage), only four female American Kestrels responded by vocalizing. One female vocalized during both the early and late nestling trials and three females only during the late nestling trials. During 11 trials, female kestrels were observed, but did not vocalize. Female kestrels uttered only klee calls, and did so at a rate of 4.5 ± 1.9 calls/min during the predator-presentation experiments. During the late nestling stage, females ($N = 4$) uttered 4.7 ± 2.2 calls/min; the only female that responded vocally during the early nestling stage uttered klee calls at a rate of 2.1 calls/min.

Overall, klee calls uttered during the predator presentation experiments consisted of an average of 14.2 ± 0.5 notes (range = 7 – 30 notes), and averaged 2.63 ± 0.28 -sec (range = 1.30-22.09 sec) in duration. I found no difference in the number of notes ($F_{1,68} = 0.01$, $P = 0.94$), duration ($F_{1,68} = 1.1$, $P = 0.40$), or frequency ($F_{1,68} = 1.7$, $P = 0.32$) of klee calls given by female kestrels at different distances from the predator (close = 2.1 – 5 m from predator vs. distant = >5 m from the predator).

Playback Experiments

I conducted 36 playback experiments at 13 kestrel nests. Both members of each pair were present during these experiments, but kestrels only vocalized during eight trials (22.2%) at seven nests. Kestrels responded to playbacks of chitter calls during

four trials (4 females and 2 males responded), of whine calls during three trials (3 females responded), and of klee calls during one trial (a male responded). Kestrels at one nest responded vocally during playback of two different calls (chitter playback, both male and female responded; whine playback, only the female responded).

One female kestrel uttered 44 of the 65 calls (67.7%) given in response to playback of conspecific calls. This female gave 23 klee calls (3.8 calls/min) in response to playback of chitter calls and 21 klee calls (3.5 calls/min) in response to playback of whine calls. Only twice did both members of a pair respond vocally, with the male and female at one nest each uttering three chitter calls in response to playback of chitter calls, and the male and female at another nest giving two whine calls and one whine call, respectively, in response to playback of chitter calls. Other kestrels that responded included a female that gave five klee calls in response to playback of chitter calls, a male giving one whine call in response to playback of klee calls, a female giving two whine calls in response to playback of whine calls, and a female giving four whine calls in response to playback of whine calls.

Overall, playback of chitter calls elicited the most vocal responses with kestrels at four nests responding (28 klee calls by females, three chitter calls by a male and three by a female, and two whine calls by a male and one by a female). Playback of whine calls elicited responses by kestrels at three nests (23 klee calls by two females, and four whine calls by a female). Only one male responded to playback of klee calls (and only uttered one call).

IV. Discussion

Call Use and Possible Functions

The most frequently uttered call by male and female American Kestrels during my study was the klee call. These calls were given at similar rates by males and females throughout the breeding season. Klee calls were uttered at the highest rates during encounters with heterospecifics, particularly humans and Red-tailed Hawks, and during intersexual interactions when the other kestrels were >5 m away. Four female American Kestrels also uttered klee calls when nests with young were approached by a 'predator' (human), and females uttered klee calls in response to playback of chitter calls (N = 2 females) and whine calls (N = 1 female).

Use of klee calls during encounters with other species near nests, particularly humans and Red-tailed Hawks in my study, suggests that they serve an aggressive function. Similarly, Balgooyen (1976:14) noted that the klee calls of American Kestrels “. . . indicate a high state of arousal and are most frequently given during inter- or intraspecific aggressive encounters . . .”

American Kestrels sometimes combine the use of klee calls with 'pendulum attacks', particularly when responding to potential predators like Red-tailed Hawks (Balgooyen 1976). During these attacks, American Kestrels dive toward the predator and simultaneously utter loud klee calls. Gard et al. (1989) presented live and taxidermic mounts of Great Horned Owls (*Bubo virginianus*) near nests of American Kestrels during the incubation and nestling periods and found that, particularly with the live owl, most pairs dived at the owl while uttering klee calls. In addition to uttering klee calls and diving, American Kestrels sometimes strike potential predators (Toland 1984).

Such behavior may effectively deter potential nest predators and, during the post-fledging period, deter predators from attacking fledglings.

In addition to deterring potential predators, the klee calls of adult American Kestrels may also serve to warn nestlings of approaching predators. For example, Dufty and Crandall (2005) broadcast klee calls near nests with 15-20-day-old nestlings and found that, in response to the calls, nestlings crouched down and reduced begging activity. Such behavior may reduce the likelihood of predation. By reducing their begging activity (including begging calls), nestling American Kestrels eliminate auditory cues potentially used by a predator to determine the presence and location of prey and, by crouching, predators reaching into nests (e.g., raccoons, *Procyon lotor*) may be less likely to capture a nestling.

American Kestrels in my study did not respond with klee calls during conspecific-presentation experiments, and only two females responded with klee calls during playback experiments. Klee calls were also uttered, although at significantly lower rates, in close intersexual contexts. In these intersexual contexts, klee calls of American Kestrels can signal aggression (Balgooyen 1976) and, although not observed in my study, klee calls may also be used in intrasexual contexts. For example, Saenger (1984) observed a female American Kestrel giving klee calls and diving at a pair that was copulating. The aggressive interaction between females (the apparent intruder and the one that had been copulating) continued for several hours, with one female eventually leaving the territory.

In intersexual contexts, klee calls can also serve a non-aggressive display function. Bowman and Bird (1987) removed mates of breeding American Kestrels to

examine the behavior of males and females during mate replacement. After mate removal, lone males and females performed aerial flight displays that involved uttering klee calls and repetitive bouts of diving, behaviors likely serving to advertise their presence to nearby, unpaired conspecifics. In support of this 'advertising' hypothesis, of 16 females whose mates were removed, eight were able to attract new mates and, of four males whose mates were removed, one attracted a new mate (Bowman and Bird 1987). During my study, klee calls given in intersexual contexts likely signaled territorial aggression, with mated pairs (i.e., not advertising for a mate) of males and females giving these calls to advertise their presence and deter conspecifics from trespassing into their territories.

Whine calls were given by both male and female American Kestrels throughout the breeding season. Most whine calls (90.8%) were uttered in distant and close intersexual contexts, with few given in apparent heterospecific contexts (9.2%). During my study, male American Kestrels sometimes uttered whine calls prior to copulating with females and both males and females uttered whine calls when incubating eggs, possibly, in the latter case, to induce their mates to assume incubation duties. Similarly, Balgooyen (1976) suggested that whine calls were given by American Kestrels when copulating, during nest relief, and when females were being fed by males. Willoughby and Cade (1964) suggested that whine calls were primarily associated with food, specifically when females begged for food from males, and only secondarily with copulation. After fledging, young American Kestrels also beg for food from adults by uttering whine calls (Lett and Bird 1987). These observations suggest that whine calls are important for communication among male, female, and fledgling American Kestrels

and, given the contexts in which the calls are used, appear to serve in soliciting the approach of a mate or, for fledglings, an adult.

Some male and female American Kestrels also uttered whine calls during conspecific presentation experiments. In experiments where I played conspecific calls at nest sites, one female responded to playback of whine calls by uttering klee calls, perhaps indicating an aggressive response to a trespassing conspecific. However, two female American Kestrels responded to playback of whine calls by uttering whine calls. The possible function of whine calls in this context is unclear, but the females might have been soliciting a closer approach to obtain additional information about trespassing conspecifics.

Chitter calls were uttered much less frequently than klee and whine calls in my study. All chitter calls were uttered by males and females in close and distant intersexual contexts, and most were given during the pre-nesting and incubation periods. American Kestrels in my study used these calls most often prior to copulating and during interactions between mates at nests during incubation, e.g., males calling as they approached nests and females calling while incubating eggs. Use of chitter calls during these interactions with mates and early in the breeding season (pre-nesting and incubation periods) suggests they play a role in pair formation and communication between mates before and after females begin incubating eggs, possibly informing mates of their approach or, as with whine calls, soliciting the approach of a mate. Similarly, Willoughby and Cade (1964) suggested that chitter calls were associated with 'friendly' approaches, frequently when one member of a pair approaches the other during courtship feeding, copulation, and feeding of nestlings. Balgooyen (1976)

indicated that chitter calls were given during sexual encounters, nest relief, and food-exchange between adults.

During conspecific presentation experiments with the study skin of a female American Kestrel, some males and females responded with chitter calls; only one female responded with chitter calls (N = 2 responses) during an experiment with the study skin of a male American Kestrel. During playback experiments, some males and females responded to playback of chitter calls by giving klee calls and, less frequently, chitter or whine calls. This use of klee calls suggests a possible aggressive response to an intruding conspecific. Kestrels responding with chitter or whine calls may, as during playback of whine calls, have been soliciting a closer approach to obtain additional information about the intruding conspecific.

Call Characteristics: Males and Females

I found no differences in the characteristics of the klee and whine calls of male and female American Kestrels. For chitter calls, mean duration was similar for males and females, but the calls of females were lower in frequency than those of males. Previous investigators have also stated that the klee calls of female American Kestrels were lower in frequency ('lower-pitched') than those of males, but provided no supporting data (Willoughby and Cade 1964, Balgooyen 1976). In addition, no one to date has provided data concerning the characteristics of the whine and chitter calls of male and female American Kestrels.

Willoughby and Cade (1964) suggested that the klee calls of female American Kestrels were lower in frequency than those of males because females are typically larger. This might also explain the lower frequency of the chitter calls of female

American Kestrels in my study. Other investigators have noted that the mass of vibrating structures, such as syringeal membranes, influences the frequency of the sounds generated (Wallschager 1980, Bowman 1983), and that body size tends to be negatively correlated with the frequency of calls and songs (Martin et al. 2011).

Call Characteristics: Effect of Nest Stage and Context

The characteristics of klee calls uttered by American Kestrels in my study did not vary with either nest stage or behavioral context. In contrast, Balgooyen (1976:14) suggested that the number of notes per klee call increased ‘in situations of stress.’ In my study, most, if not all, klee calls uttered by American Kestrels appeared to signal aggression in both intra- and heterospecific contexts. If so, then a possible explanation for the lack of variation in the characteristics of klee calls in my study is that the behavioral contexts in which they were uttered did not vary.

As with klee calls, characteristics of chitter and whine calls uttered by American Kestrels in my study did not vary with either nest stage or behavioral context. Such results suggest that American Kestrels do not vary the characteristics of these calls to convey different information to conspecifics.

V. Summary

In summary, I found that male and female American Kestrels used three different vocalizations (klee, chitter, and whine calls). During observational studies I found that sex had very little effect on characteristics of vocalizations, with the exception of chitter frequency, with males having a higher frequency than females. Sex and call context had a significant effect on use of calls and number of calls per bout, with klee calls being used significantly more frequently and containing more calls per bout during heterospecific contexts than either close or distant intersexual interactions. Call context affected whine calls with more calls given during close and distant intersexual interactions than during heterospecific interactions. Additionally, during heterospecific interactions, females uttered more calls per bout than males. Analysis of how male and female American Kestrels use and vary the characteristics of their calls during different breeding stages and in different behavioral and experimental contexts improves our understanding of their function and how kestrels might vary call characteristics to convey information to conspecifics.

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