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THE CALLS AND ASSOCIATED BEHAVIOR OF BREEDING WILLOW PTARMIGAN IN CANADA

KATHY MARTIN,[1] ANDREW G. HORN,[2] AND SUSAN J. HANNON[3]

ABSTRACT.—We describe the physical structure, use, and possible functions of 11 calls of breeding Willow Ptarmigan (*Lagopus lagopus*), most of which were given by both sexes. Both sexes had visually and acoustically conspicuous territorial calls (flight song, rattle, "kohwa," and "aroo" (males only). "Koks," "ko-ko-ko," and "krrow" were given by both sexes as low intensity threat, territorial, or sexual situations, or to maintain contact with the mate or offspring. "Purr" and "moan" were given usually by females to communicate with chicks, and "hiss" and "scream" calls by both sexes in intense defence of offspring or mates. The sex of the caller was usually easily recognizable, as males had strong and rapid amplitude modulations in their calls, which females lacked. The most complex calls were flight songs which consisted of several calls in sequence. Unlike other nonpasserines, Willow Ptarmigan do not appear to have a repertoire of calls that are graded variants of one another. Calls of North American populations of Willow Ptarmigan appear similar to those of European populations. *Received 2 June 1994, 5 Mar. 1995.*

The social systems of grouse (Phasianidae: Tetraoninae) have been well studied (Hjorth 1970, 1976, Wiley 1974, Wittenberger 1978, Johnsgard 1983), but their vocal repertoires are poorly described, with few complete vocal ethograms that include sonograms for both sexes, but see Stirling and Bendell (1970). Ptarmigan are particularly interesting because they are one of the few monogamous members of the subfamily Tetraoninae. Willow Ptarmigan (*Lagopus lagopus*) males provide parental care, and after the eggs hatch, they can raise young on their own (Wittenberger 1978, Martin and Cooke 1987). Thus, members of Willow Ptarmigan pairs and broods are in frequent vocal contact during the breeding season. Qualitative descriptions of the calls of Red Grouse (*L. l. scoticus*) in Scotland have been reported by Watson and Jenkins (1964). Cramp and Simmons (1980) provided sonograms for several of these calls. In Norway, several territorial and mating calls of free-living birds of the continental European subspecies (*L. l. lagopus*) are described (Pedersen et al. 1983, Johnsen et al. 1991), and Wike and Steen (1987) described four parental calls, three with accompanying sonograms of three captive brood hens. The calls of North American Willow Ptarmigan have not been described. In this paper we describe the calls of free-living breeding birds in northern Canada and provide details on the context of their use.

[1] Canadian Wildlife Service, 5421 Robertson Rd., R.R. #1, Delta, British Columbia, Canada, V4K 3N2, and Dept. of Forest Sciences, Univ. of British Columbia, 2357 Main Mall, Vancouver, British Columbia, Canada, V6T 1Z4.
[2] Biology Dept., Dalhousie Univ., Halifax, Nova Scotia, Canada, B3H 4J1.
[3] Dept. of Zoology, Univ. of Alberta, Edmonton, Alberta, Canada, T6G 2E9.

METHODS

Calls of Willow Ptarmigan were recorded at two sites in northern Canada: a population of *L. l. albus* (Johnsgard 1983) at La Perouse Bay (LPB) (58°24′N, 94°24′W), 40 km east of Churchill, Manitoba (Martin 1984) and a population of *L. l. alexandrae* (Johnsgard 1983), 2500 km west of LPB, at Chilkat Pass (CP) in northwestern British Columbia (59°50′N, 136°30′W) (Hannon 1983, 1984). The general biology, behavioral ecology, and life history of both of these Willow Ptarmigan populations have been documented elsewhere (Hannon 1983, 1984, Martin 1984, Martin and Cooke 1987, Martin et al. 1989, Hannon and Martin 1992, Mossop 1988). At both sites, males arrived on territories in mid- to late April, shortly before females. Nests were visited every 2–4 days until hatch or clutch failure (Hannon et al. 1993). During the breeding season most individuals can be approached within 10 m and less than 3 m for birds with nests and broods. Pairs remain together until mid-August or through September.

At LPB, we conducted 49 recording sessions of one or both members of 17 pairs (13 males, 16 females) during 18 Jun.–4 July 1984. Color-marked individuals were recorded one to four times. We described the behavior accompanying the vocalization and the response of the mate, the offspring, or neighboring birds to the individual vocalizing at each session. To establish further the behavioral context of parental vocalizations, we conducted watches at 22 nests from blinds placed 8–10 m away during late incubation and the first day of brooding in 1982 and 1983. During the breeding seasons of 1981–84, we made opportunistic observations of vocalizations and contextual behavior from mid-April to mid-August. As a consequence of female removal experiments at hatch (Martin 1987, Martin and Cooke 1987), we were able to obtain recordings of a range of male parental calls that would not be readily observed in bi-parental pairs. At CP, both sexes of ptarmigan were recorded during territorial establishment in late April and early May 1980, 1981, and 1986. By combining recordings from both sites, we assembled a comprehensive vocal repertoire for both sexes of Willow Ptarmigan during the breeding season. Where possible, we used the descriptions of Watson and Jenkins (1964) as a reference.

Initial categorization of calls was by ear during fieldwork by KM (LPB) and SJH (CP). In the laboratory, AGH listened to the field tapes and analyzed at least one example of each category of call (one or a series of notes) encountered for each individual. Calls were considered to belong to different categories if the difference between them was qualitative rather than quantitative. Thus, categories differed in whether they were frequency modulated or not, had one note or not, etc. An over-estimate of the number of call categories would result from this method if, for example, a particular individual had an aberrant call or if intermediates between call types were missed. We are confident this did not occur in our study. However, we may have under-estimated the number of categories because we pooled calls that could have been distinguished using quantitative measures of their acoustic characteristics. Although it is possible that our tape machine missed all or parts of calls, we were able to tape very low amplitude calls such as quiet "moans" (see Fig. 4B).

Vocalizations were digitized using SoundWave software at nine bits and a sampling rate of 22 kHz. The resulting files were converted to 12-bit files and analysed using MacSpeech Lab II software. For purposes of illustration, we selected clean recordings that gave a range of variation in the calls or that clearly showed the typical features of the call type. These were produced using Canary 1.1 software at a filter bandwidth of 705 Hz, analysis bandwidth of 173 Hz, and a time resolution of 1.4 ms.

RESULTS

Koks.—"Kok"s were short (about 50 ms) calls that were strongly sexually dimorphic (Fig. 1A, B). In males, calls showed rapid amplitude

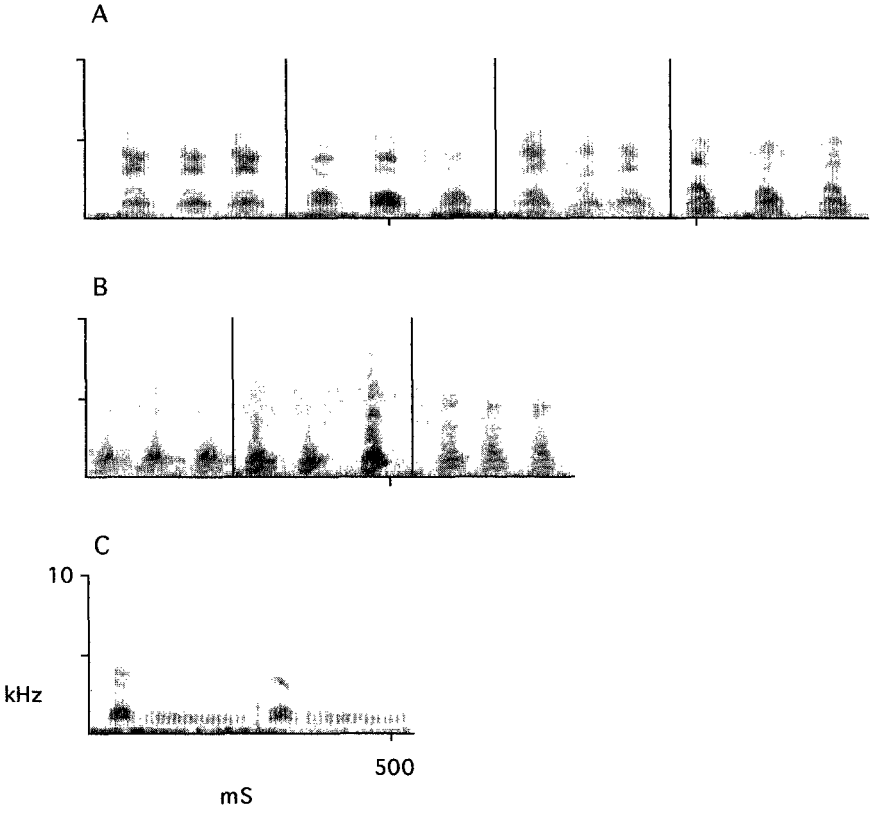

FIG. 1. Willow Ptarmigan: A—three "kok"s from each of four males; B—three "kok"s from each of three females; C—two "ko-ko-ko"s from one male. Vertical lines separate individuals. Note differences between as opposed to within individuals in both A and B.

modulation (pattern of loud and soft sounds) with a fundamental frequency that usually remained around 1000 Hz and that had a sharp onset and termination, showing sidebands that appeared to be formants (broad horizontal bars, sometimes indistinct) rather than harmonics (equidistant horizontal bars, generally narrow). In females, they were less strongly amplitude-modulated and showed two to six distinct harmonics. The frequency modulation of the calls were downward, upward, or up and down (chevron-shaped), depending on the individual and possibly on the situation. The abruptness and rapid amplitude modulation of male "kok"s (Fig. 1A) made them sound like "bek"; the smoother envelope (overall pattern of loudness) of female "kok"s (Fig. 1B) made them sound like variants on "cluck."

"Kok"s were given in prolonged bouts while paired birds were foraging near one another, during territorial and sexual interactions, and when intruders (predators or humans) were close to nests or broods. We observed more intra-individual variation in female "kok"s than in males (Fig. 1A, B). This call may indicate general arousal, as they were used both as contact calls and to indicate the presence of a potential threat. The rate of delivery varied from about 20 to 120 per minute. The rate of delivery and the abruptness of their onset and termination may be a graded signal of the intensity of the arousal (e.g., with the approach of a predator). Watson and Jenkins (1964) noted that amplitude, sharpness of onset and termination, and rate of delivery appeared to increase with speed of aerial chases and with intensity of response to a predator at the nest. They classified the variation in the structure of this call into two categories, "chase kok"s and "warning kok"s. More detailed analyses of our populations might support such divisions.

Ko-ko-ko.—This was a low amplitude call given in prolonged bouts, often with several "ko" notes strung together (Fig. 1C). They had a relatively low fundamental frequency (below 1000 Hz) and were rapidly amplitude-modulated, basically making them low growls or "purr"s. "Ko-ko-ko" calls were given by males in low level alert postures and were not specifically associated with any one behavior. Watson and Jenkins (1964) suggested that they were flight intention calls. They may be homologous to female "purr"s.

Krrow.—These were medium length (50–300 ms) calls that rose quickly and fell slowly in frequency (Fig. 2A, B). In males, they were rapidly amplitude-modulated with a fundamental frequency of about 1500 Hz that varied by about 30 Hz throughout the call (Fig. 2A). Two to three formants were present in males; a shift in their emphasis to higher frequencies about one-third through the call made them sound like "bugow". In females, the initial rise in frequency was more abrupt, and several harmonics were apparent, making the call sound like "meow" (Fig. 2B). "Krrow"s were sometimes given singly but were usually in bouts of two to five calls.

"Krrow"s were frequent during intra-sexual territorial encounters, during which calls were exchanged rapidly between neighboring males or females along with "kohwa"s (especially between males). "Krrow"s were also used to regain contact with mates and young. Females gave "krrow"s after their mate left them temporarily during the pre-incubation period in eight out of nine cases at LPB in which females vocalized; these calls stopped when the male returned. At CP, males frequently flew to their mates when females gave "krrow"s. During brood rearing, they were usually given by the parent to dispersed chicks. The calling bird uttered

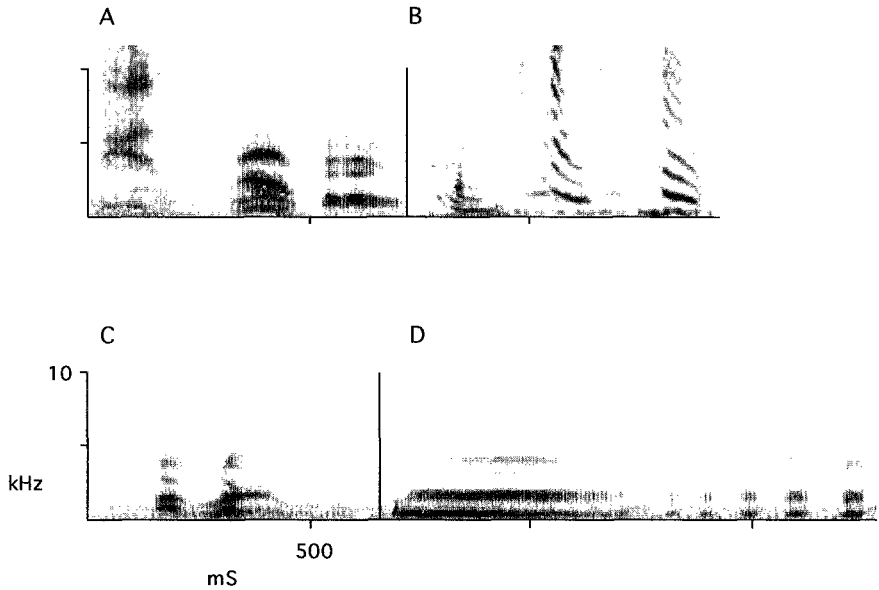

FIG. 2. Willow Ptarmigan: A—"krrow"s of three males; B—"krrow"s of three females; C—"aroo"; D—the next "aroo" given by the same male, trailing off into a "rattle".

"krrow"s at a rate of 2–30 per minute until all the chicks had gathered, after which the calls stopped abruptly. Watson and Jenkins (1964) described the "krrow" as a threat and contact call used for intra-sexual aggression and for establishing or maintaining contact within pairs and with young. Johnsen et al. (1991) referred to the "krrow" as a "weak threat" call but also indicated that Norwegian Willow Ptarmigan used this call in social and sexual situations.

Kohwa.—"Kohwa"s were amplitude-modulated, medium length (about 100 ms) calls with a distinctive overall pattern of frequency modulation—a brief up and down followed by a longer up and down pattern and a flat terminal portion, changing by about 500 Hz (call shown in latter half of Fig. 3C).

"Kohwa"s were most commonly given in territorial encounters, when rapid bouts of calls were exchanged between males in alternation with rapid bouts of "krrow"s. In these bouts they were sometimes given in a series and sounded like "gowayogowayo . . ." They also formed the terminal portion of flight songs (Fig. 3C) and were given during strong responses to disturbance by intruders at nests (Martin 1985, Hik et al. 1986). Females occasionally gave this call at CP during border disputes. "Kohwa"s given singly or in strings did not differ enough to qualify as

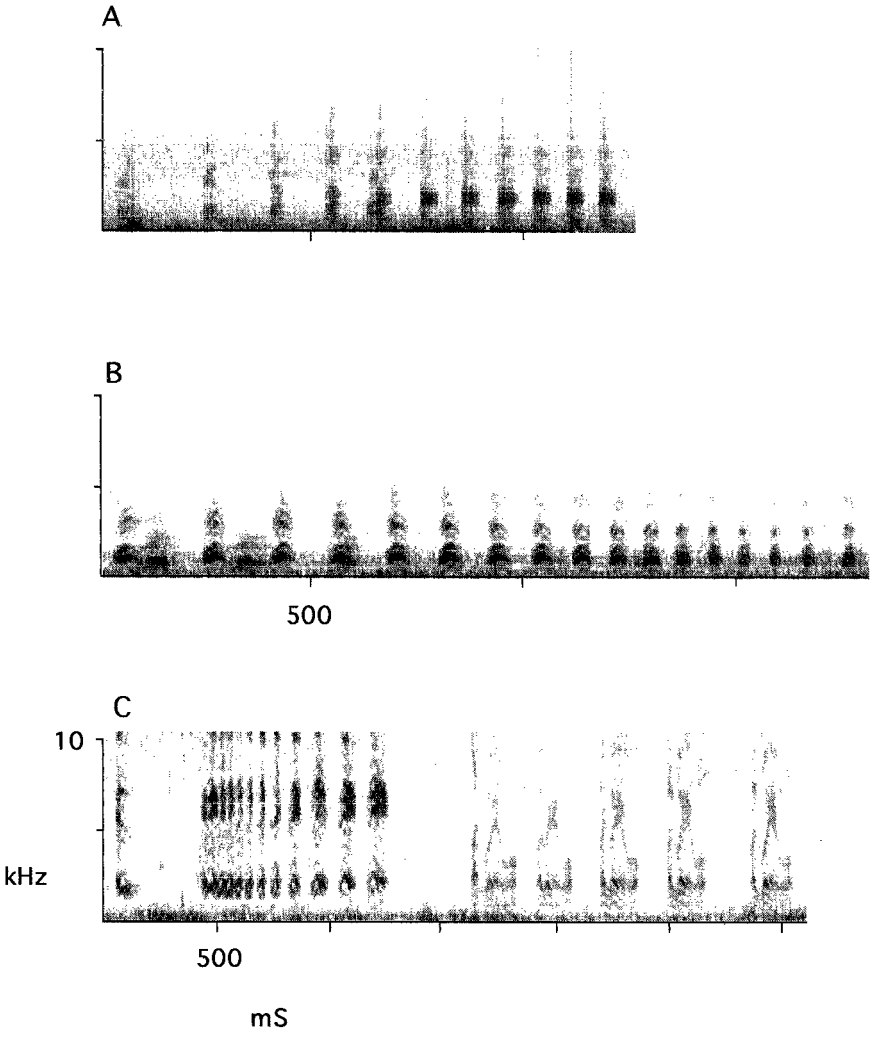

FIG. 3. Willow Ptarmigan: A—"rattle" of a male; B—"rattle" of a female; C—"flight song" of a male.

separate categories by our criteria, and they occurred too infrequently during the nesting period for us to determine differences in their use. In European populations, "kohwa" and "kohway" calls are described as attack and attack intention calls (Watson and Jenkins 1964, Johnsen et al. 1991).

Aroo.—"Aroo" was a highly variable call, with an overall falling and

rising pattern of frequency modulation and rapid amplitude modulation at a varying rate and intensity (Fig. 2C, D). An initial medium-length (500 ms) note was usually followed by shorter notes with indeterminant structure, usually similar to the initial note but chevron-shaped. "Aroo"s sometimes formed a graded series with "kohwa"s and were combined with other calls (e.g., "rattle"s, Fig. 2D) during intense territorial encounters.

Observations early in the breeding season at LPB suggested "aroo"s were given by males in the most intense territorial disputes and frequently preceded physical aggression. "Aroo"s occurred less frequently during the nesting period but again were associated with intense defense of offspring by males (Martin 1987).

Rattle (song on the ground).—The rattle was a long accelerating string (800 ms) of short elements that were quite similar to "kok"s and may be modified versions of them (Fig. 3A, B). As in other calls, elements showed rapid amplitude-modulation in males (Fig. 3A), giving them a harsher quality than calls of females (Fig. 3B).

Both sexes gave "rattle"s spontaneously or in response to the "rattle" of another male or to "krrow"s by females. "Rattle"s were one of the more common male calls for low intensity territorial advertisement and defence, especially in early spring and at dawn later in the breeding season. Females at CP gave "rattle"s fairly commonly at dawn in early spring shortly after they arrived on territory, often in response to hearing or seeing another female on their territory.

"Rattle"s were also given when intruders entered a territory, approached a nest, or when one of the pair was flushed by an observer. In such instances, they were almost always preceded by high rates of "kok"s. The association with accelerating bouts of "kok"s, suggested that the "rattle" was given during an increased state of arousal.

Flight song.—The vocalization given during territorial flight displays was a two-part series of calls (Fig. 3C). The first part was a decelerating series of what appears to be modified "ko-ko-ko"s and the second consisted of "kohwa"s. The notes in the first section of the flight song were chevrons with a peak frequency of 2000–2500 Hz and length of 26–31 ms. The first and second note in the first part of the flight song were separated by a pause, the next two to four notes ran together, and the following six or more notes decelerated and lengthened. The second part of the flight display consisted of decelerating "kohwa"s.

Flight songs occured in several situations. They were given by both sexes during territorial advertisement, most frequently at dawn or after territorial encounters. Flight songs by one individual often stimulated flight displays among neighbors, in a manner similar to the songs of many

passerines. Abbreviated flight songs, without "kohwa" elements, were frequently given when males were disturbed from resting or hiding sites. Flight displays also occurred when males rejoined their mates after a brief absence and during nest defense, particularly upon the return of the male to the nest site. During forced choice experiments, many males at LPB preferentially defended their female rather than their eggs during early incubation (Martin 1984). In these tests, males that chose to defend their mates gave flight songs, but males that defended their offspring did not (KM, unpubl. data). At CP, females gave flight songs in early spring when they heard or saw another female on their territory. This behavior ceased when egg laying commenced.

Flight songs were the most complex of the ptarmigan calls we measured. When given spontaneously, they appeared to correspond in function to the songs of other bird species, notably shorebirds and passerines, in broadcasting information about territory ownership, and without being directed to specific individuals or associated with specific interactional behaviors. When used upon returning to the mate, they may function in the same capacity as greeting ceremonies in Anseriformes and Psittaciformes. As in these analogous behaviors, the complexity of the call may identify the individual, but their complexity seems excessive for this function alone and may indicate the singer's quality as well.

Purrs.—Heard only from females, "purr"s were short, low frequency (c. 800 Hz), irregular trains of pulses (loud part of note) that rose and then fell in frequency over about 50 Hz (Fig. 4A). They varied greatly in amplitude but without obvious changes in the details of their structure. During a disturbance at the nest, "purr"s were given in similar situations to "kok"s and usually when "kok" rates were high. In this situation, a "purr" appeared to be an alarm call of higher intensity than a "kok" but lower than a "hiss". "Purr"s were also given when females returned to their nests after an incubation recess or after being flushed from the nest during incubation and hence may advertise attachment to the nest site.

Moan.—"Moan"s are low frequency, medium length calls with relatively few harmonics and, unlike most ptarmigan calls, lack amplitude modulation (Fig. 4B). "Moan"s were heard mainly from females and were given singly or in bouts, sometimes being introduced without pause by a "kok", making a "kok-moan." "Moan"s were given when females gathered their chicks for brooding or moved them away from the site of a disturbance. This call appeared to function as a "come hither" command since young chicks responded immediately to the "moan" by approaching and following the female. When we imitated the "moan", chicks less than five days of age emerged from cover and approached us,

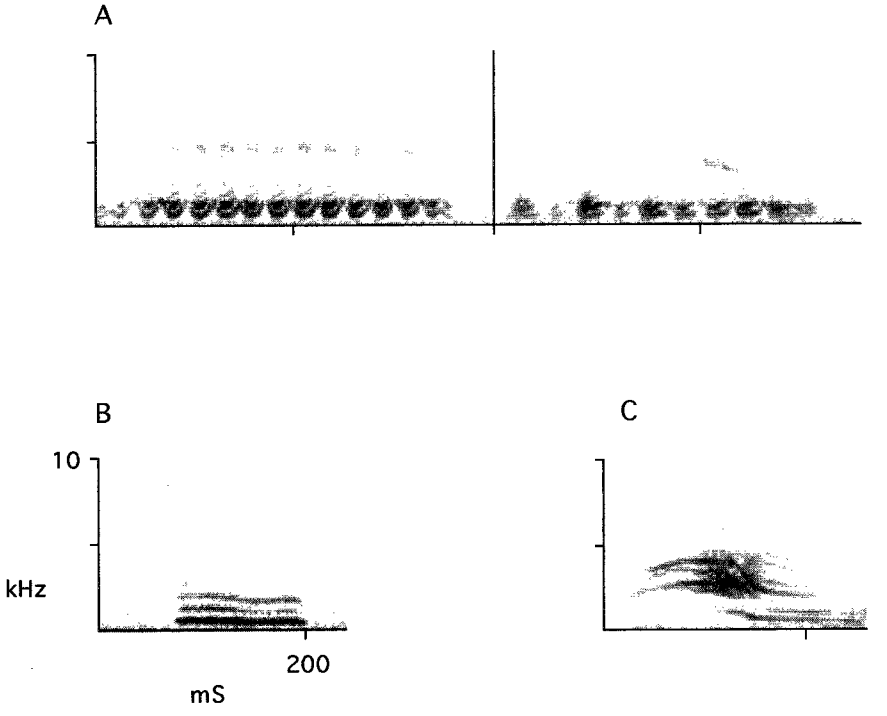

FIG. 4. Willow Ptarmigan: A—"purr" of two females; B—"moan" of a female; C—"scream" of a female. Vertical lines separate individuals.

sometimes walking over our feet or legs or our bird dogs to approach the calls. Older chicks moved from their hiding place but stopped when they saw us. We lacked a sufficient sample of females to examine individual variation in the "moan", but Allen et al. (1977) indicated that chicks recognized their mothers' call. We observed little mixing of wing-tagged chicks between broods in either population. Possibly, the "moan" assists in brood cohesion as well as a call to gather.

Scream.—This was a noisy call with an indeterminate harmonic structure, a relatively high fundamental frequency, and given in brief, loud bouts (Fig. 4C). "Scream"s were given in distress situations when females were suddenly flushed from the nest and by both sexes during intense defense of nests or broods. A male single parent gave "scream"s as he attacked a female Northern Harrier (*Circus cyaneus*) that approached his brood of 10 two-day-old chicks (Martin 1987).

Hiss.—A "hiss" (not illustrated) was a band of white noise about 2 s long and was given during distraction displays. Parents of both sexes were

observed to "hiss" when disturbed at the nest or with young chicks. Occasionally, adults and chicks several weeks old "hiss"ed when being held by observers.

DISCUSSION

The vocal repertoire of Willow Ptarmigan in North America consists of at least 11 calls, most of which are given by both sexes and in both populations. We did not attempt to compare the calls or the context between our two populations because of our limited sample of many calls and because the emphasis in our respective studies differed, resulting in different opportunities to record various calls and to observe the contextual behavior. For example, female "rattle"s were heard more frequently at CP than at LPB, perhaps because the density of birds was higher at CP (Hannon et al. 1988) or possibly because there was more emphasis on territorial behavior, especially of females, in the CP study (Hannon 1983, 1984) compared to the LPB study. Most parental calls for both sexes were recorded at LPB, given the emphasis on parental behavior in this study (Martin 1987, Martin and Cooke 1987).

In several cases, call types such as "purr", "moan" and "aroo" were given predominantly by one sex. In some instances, this may relate to the opportunities to record such calls. For example, during brood rearing females do most of the vocal communication to young chicks. We were able to sample the repertoire of male parental calls more completely in our study as a consequence of experiments at LPB where we removed female parents on the day of hatch (Martin 1987, Martin and Cooke 1987). During watches, we heard single parent males use modified (lower and softer) "kok"s, "krrow"s, and "ko-ko-ko"s to communicate with their day-old chicks, but we did not hear them give calls equivalent to the "moan" or "purr". However, all watches were done within several hours of the hen removal, and it is possible that single parent males developed these brood contact calls later. Most single parent males successfully raised several of their offspring (Martin and Cooke 1987).

We observed several additional calls that we were unable to record. There were calls to warn of the approach of avian or mammalian predators; the response of the mate or chick is to freeze or to run for cover and then crouch. At both sites, we heard birds give separate calls to warn of approaching avian and mammalian predators. Watson and Jenkins (1964) described the avian predator call as a "chorrow," and they observed birds giving a loud and high pitched "kok" to warn of approaching mammalian predators. We have not observed females give food calls to attract chicks to food sources at either LPB or CP, but these likely exist. In captivity, a two-syllable food call ("ku-ku"), similar to the "tid-

bitting" food call used by domestic poultry, was given by Willow Ptarmigan brood hens in Norway (Wike and Steen 1987), and Scottish Red Grouse chicks responded to the food calls of domestic poultry foster parents (Watson and Jenkins 1964). Food calls have been observed for wild North American White-tailed Ptarmigan (*L. leucurus*) (Braun et al. 1993).

Several ptarmigan vocalizations appear specialized for reunion of family members and for crisis situations such as predator intrusions. Individuality in "kok"s and "krrow"s, for example, was apparent both on sonograms and to our ears, although our data set precluded a detailed analysis of this. Most calls showed relatively sharp onsets and wide frequency ranges, features that should make them easy to locate. The "moan", "ko-ko-ko", and "purr" were exceptions to this rule and were often given at low amplitude when the caller's apparent intent was to remain cryptic.

Most Willow Ptarmigan calls were strongly sexually dimorphic, even to our ears. Male calls were consistently strongly amplitude-modulated, and their calls generally showed formants rather than the harmonics seen in female calls, suggesting that the sexes produce their calls differently. From a functional perspective, males may give more abrupt, broad spectrum calls that are easier to locate (Marler 1955) than females in the presence of predators because males wish to lead predators from the vicinity of their nests or broods (Hannon and Martin 1992).

Most grouse species show little parental care by males and large sexual dimorphisms in plumage and displays (Wiley 1974). Willow Ptarmigan deviate from this general pattern by showing extensive male care (Martin and Cooke 1987) and less sexual dimorphism. Sexual dimorphism in calls is also less pronounced for Willow Ptarmigan than for other grouse species (Cramp and Simmons 1980, Johnsgard 1983). Willow Ptarmigan form long term pair bonds, and thus male calls serve territorial, sexual, social, and parental functions. Also, female Willow Ptarmigan are territorial and show intra-sexual aggression (Hannon 1983, Martin et al. 1990). The monogamous bi-parental mating system of Willow Ptarmigan results in the need for members of pairs to communicate with each other and their offspring thoughout the breeding season. This may explain the almost complete sharing of calls by both sexes of Willow Ptarmigan compared to other members of the Tetraoninae.

Different observers might classify calls differently, thus making the absolute repertoire size of a species difficult to compare with that of other groups or populations. Also, there is the additional complication of asymmetric opportunities to sample calls equivalently for both sexes and throughout the breeding season. However, our classification for Willow

Ptarmigan broadly agrees with that of Watson and Jenkins (1964). Except for the "kohwa-aroo" series of calls, we found no obvious intermediates between the call types we described, unlike the majority of other studies of calls in nonpasserines (e.g., Jenni et al. 1974, Huxley and Wilkinson 1977, Clapperton and Jenkins 1984, Collias 1987). If our estimate of repertoire size is correct, Willow Ptarmigan have a mid-sized repertoire compared to other nonpasserines. Compared to other Tetraoninae, ptarmigan have the largest repertoire of calls, and Willow Ptarmigan appear to have the greatest amount of overlap of calls used by both sexes (Cramp and Simmons 1980, Johnsgard 1983).

Willow Ptarmigan are an excellent species to conduct detailed studies of vocalizations in relation to the behavior, genetics, and life history of individuals since they are easy to approach, record, and observe. Multiple recording sessions of individuals are possible, and most individuals and their relatives in a population can be sampled. High male natal philopatry (Martin and Hannon 1987) would allow examination of the heritability of calls such as "kohwa," "kok," "ko-ko-ko," "krrow," "aroo," "rattle," and "flight song." Finally, variation in calls could be examined in relation to mate choice, social behaviors, and life history consequences.

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