

VOCALIZATIONS OF COOPER'S HAWKS DURING THE PRE-INCUBATION STAGE¹

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Abstract. From 1986 to 1990 we studied the vocalizations of 10 mated pairs of Cooper's Hawks (*Accipiter cooperii*) during the pre-incubation stage. We heard four different vocalizations during nest-building, copulatory, and other pre-laying activities. There was a marked asymmetry in vocalizations between the sexes during the pre-incubation period. Compared to males, female Cooper's Hawks (1) had a larger repertoire of calls, (2) called more frequently, and (3) called during a wider array of activities. We suggest that the various calls signal presence, identity, location, dominance, and non-aggressive motivation. We attribute some of the intersexual differences in pre-incubation vocalizations to the pronounced degree of reversed sexual size dimorphism in this species.

Key words: *Accipiter cooperii*; Cooper's Hawk; vocalizations; pre-incubation behavior; intersexual behavioral differences; reversed sexual size dimorphism.

INTRODUCTION

Research on pre-incubation behavior of raptors in the wild has been largely neglected (Newton 1979), and information on the vocal repertoires of falconiforms is mostly lacking (Palmer 1988). Vocalizations may be a primary means of communication for Cooper's Hawks (*Accipiter cooperii*) during the pre-incubation period because mated pairs conduct most of their mutual activities in relatively dense woodland vegetation where visual contact is limited (cf. Smith 1972, Jellis 1977, Ficken et al. 1978). During 1986-1990 we investigated the pre-incubation behavior of the Cooper's Hawk in Wisconsin (Rosenfield 1990). Here we describe the vocalizations of mated pairs at this stage of breeding, the circumstances in which these calls were given, and the possible functions of such vocalizations.

We focus in particular on intersexual differences in vocalizations. Male-female interactions in the pre-incubation period may involve complex behavioral adjustments between the pair members, and this may entail a strong selective force on vocalizations (Lein 1980). In most spe-

cies, courtship behavior includes a process to accommodate or reduce aggressive behaviors (Ratcliffe 1980). This may be especially true for birds of prey because of their morphological adaptations and strong motivation for killing (Wrege and Cade 1977). Forming and maintaining pair bonds may be particularly difficult for strongly dimorphic raptors. Male birds of prey (including Cooper's Hawks) often seem intimidated by or reluctant to approach their larger mates (Wrege and Cade 1977; Snyder and Wiley 1976; Newton 1986, pers. observ.). In Wisconsin, female Cooper's Hawks are about 1.6 times heavier than males and appear to dominate their mates (Rosenfield and Bielefeldt, unpubl.), as in other raptor species (Mueller 1986). Females may send messages to their smaller mates that signal non-aggressive motivation, elicit approaches, and facilitate mating (i.e., copulation). We suggest that some of these messages are vocal.

The only detailed descriptions (Brown and Amadon 1968, Palmer 1988) of the vocalizations of the Cooper's Hawk are based on Meng (1951). He gives a narrative summary of activities during the pre-incubation stage, but his observations are unquantified and sample sizes typically are not provided. Although some of our results are similar to Meng's, others are not.

STUDY AREAS AND METHODS

We noted all vocalizations of 10 mated pairs of Cooper's Hawks during single observational ep-

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isodes at 10 randomly chosen nesting areas in central and southeastern Wisconsin during March and April 1986–1990. A nesting area is defined as that relatively small area (ca. 300 m in diameter) within which a mated pair conducts most breeding activities, except foraging, in a given year (Rosenfield 1990). Identification of such sites was based on an 11-year data set (Rosenfield and Bielefeldt, unpubl.).

All birds at the 10 nesting areas were different (marked) individuals and all were in adult (grey) plumage. All observations were made after pair formation and all mated pairs laid eggs. Observations were conducted 7–17 days before laying of the first egg in most (8) cases, and 30–32 days before first egg in remaining cases.

We watched Cooper's Hawks for a total of 25.4 hr from blinds erected within 70 m of uncompleted nests. All observational episodes began at dawn with the day's first arrival (04:30–05:00) of an adult near a nest. Episodes varied in length (28–570 min) according to the duration of both sexes' presence on the nesting area. It is unlikely that we disturbed the hawks when we entered the blinds before dawn, as most birds did not appear to roost near (≤ 50 m) nests and we never detected them when entering the blinds. Time and duration of behavioral patterns were recorded (to the nearest sec or min) whenever possible, or else estimated. Distances were paced, measured on 1:4,800 aerial photos, or estimated.

Sex was determined by the pitch of vocalizations (excluding copulation calls, male calls are usually higher [pers. observ.]) and, when possible, by size (males are markedly smaller). On 25 April 1988 in Waupaca County, Wisconsin (44°20'N, 89°14'W), we tape-recorded the calls of one pair with a 3M 880 Wollensack cassette recorder and a Dan Gibson parabolic microphone (copy on deposit at Cornell University's Library of Natural Sounds). Sound spectrograms of the calls were produced with a Multigan Uniscan II Spectrograph.

The data reported here extend and complement studies during 76 additional observational episodes at 20 other nesting areas (Rosenfield 1990). For logistical reasons we could not catalog all vocalizations in these other 76 episodes, but the patterns of vocal behavior observed at these sites accord in all respects with the results from the 10 nesting areas analyzed here. We occasionally refer to the data from these additional sites.

Vocalizations discussed here occurred during

a stereotypical schedule of events, summarized as follows (for additional details see Rosenfield 1990). After activities at dawn, described below, nest building begins. Only one bird builds at a time and sticks are collected within about 80 m of the nests. The other bird remains nearby, occasionally changing perches within about 40 m of the nest and its mate. Building continues for a variable portion of the morning (the peak of daily courtship activities occur in the morning over about 30 days [Rosenfield 1990]), and several copulations usually ensue at this time. Females remain on nesting areas throughout the day; males are absent several times a day while procuring food for themselves and their mates (Rosenfield 1990). Females may call 2–4 times/hr during male absences (pers. observ.), a rate much reduced from the median rate of 36 calls/hr (range = 9–288) observed during mutual presence of the 10 pairs analyzed here. All of the vocalizations tabulated here, however, were given while both sexes were present on the nesting area.

Although not considered here, calls and behaviors associated with the transfer of food from males to females are similar in all stages (preincubation through early fledging) of the nesting cycle (pers. observ.).

Some of our terminology and classification follow previous descriptions of falconiform courtship (Wrege and Cade 1977, Ratcliffe 1980, Feldsine and Oliphant 1985).

RESULTS

All birds vocalized at least twice during observational episodes and each female called more often than her mate (Sign Test, $P < 0.01$, $n = 10$) (Table 1).

All birds called immediately upon their appearance at the nesting area at dawn. Males called first on six occasions. In all cases, the opposite member of the pair started calling within 1 min of the beginning of its mate's calls. Males always called from a perch; their initial calling posts were 30–100 m from the nest. Females' initial calling positions were difficult to determine because five females called while in flight toward the nest or the male's position. All were approximately 80–200 m from their nests when they began calling. Median male-to-female distances at initial calls was ~ 65 m ($n = 10$, range = 30–200 m), similar to a median of 60 m reported for 28 morning episodes in Rosenfield (1990).

TABLE 1. Total calls (excluding copulation calls) and circumstances of vocalizations by Cooper's Hawks during 10 observational episodes during pre-incubation.

Episode	Total no. calls (% at dawn)		% nest visits (n) with calls	
	Males	Females	Males	Females
1	27 (100)	134 (8)	0 (1)	38 (8)
2	9 (100)	120 (14)	0 (14)	100 (8)
3	14 (71)	119 (18)	50 (2)	100 (3)
4	8 (100)	20 (60)	0 (2)	100 (1)
5	4 (50)	32 (63)	20 (10)	100 (2)
6	24 (88)	82 (26)	25 (8)	20 (5)
7	14 (71)	510 (4)	25 (8)	100 (3)
8	2 (100)	85 (34)	0 (45)	40 (62)
9	15 (73)	99 (8)	12 (25)	100 (11)
10	16 (94)	136(10)	2 (45)	44 (9)
Total	133	1,337		
%	(85)	(25)	13	74

Males only gave "kik" calls (see Fig. 1); females gave "kik" calls, "cak-cak-cak" calls, and "whaaa" calls (see Figs. 1-3 and Table 2).

We heard four different vocalizations: (1) single noted "kik" calls, aurally similar to the male's prey delivery call (Fig. 1); (2) multi-noted "cak-cak-cak . . ." calls, similar to alarm or nest defense calls and often pre-fixed by or interspersed with one or more isolated "kik" notes in females (Fig. 2); (3) slow, whining "whaaa" calls resembling vocalizations of the Gray Squirrel (*Sciurus carolinensis*), in clusters of 1-4 notes (Fig. 3); and (4) multi-noted copulation calls, which sounded like quick, abbreviated "whaaa" calls (Fig. 4). We never heard the long (ca. 10 sec), drawn out single 'whaaa' copulation call described by Meng (1951). Copulations ($n = 36$) during the 10 episodes analyzed here never exceeded 6 sec (the same is true for 93 other copulations observed in episodes not analyzed here—see Methods). Females called during all 36 copulations, males during 30.

Males gave only "kik" and copulation calls. Although there was variability among males in duration of calling (1-7 min) and total number of calls (2-27) at dawn (i.e., beginning with their daily arrival on nesting areas and preceding nest building), 85% of total male calls occurred during relatively brief periods at dawn (Table 1). Of the remaining 18 "non-dawn" calls, 10 occurred on the first or second visit to nests by males that day. We never heard males give "cak-cak-cak" calls at dawn, as reported by Meng (1951), nor did we hear the extended male and female "duets"—up to an hour in length at dawn—described by Meng (1951).

Males did not call while in flight, while collecting twigs for nests, nor did they call while

females were collecting twigs, or when females were at nests. Except for vocalizations during their arrivals at dawn, during copulations, and during their first few nest visits of the day, males were almost completely silent while in the presence of their mates.

Nine of 10 females gave "kik" calls too, but in contrast to males, all of them also used "cak-cak-cak" calls and most gave "whaaa" calls (Table 2). As with males, there was variability in the total number of calls (8-29) given by females at dawn. But a mean proportion of only 25% of total female calls (vs. 85% for males) occurred during the time that males called at dawn (Table 1). Eight females used "kik" calls at dawn. A mean proportion of 60% of total female "kik" calls occurred at this time (Table 2). Eight females also used "cak-cak-cak" calls at dawn (Table 2); a mean proportion of 55% of total female "cak-cak-cak" calls occurred at dawn. Five females used two different calls (and one used three calls) at dawn (Table 2). Two "whaaa" calls given by one female at dawn (Table 2) were not her initial calls.

Females vocalized significantly more often than males during nest visits (Sign Test, $P < 0.02$, $n = 10$)—mean proportions of 74% for females vs. 13% for males—and six females called on every nest visit (Table 1). Six females called (1-12 times) while in flight (either approaching the nesting area at dawn and/or when switching perches near nests). Nine females called while males were nest building: four gave 2-32 "kik" calls, five females gave 2-22 "cak-cak-cak" calls, and six gave 2-ca. 200 "whaaa" calls. Six females called while

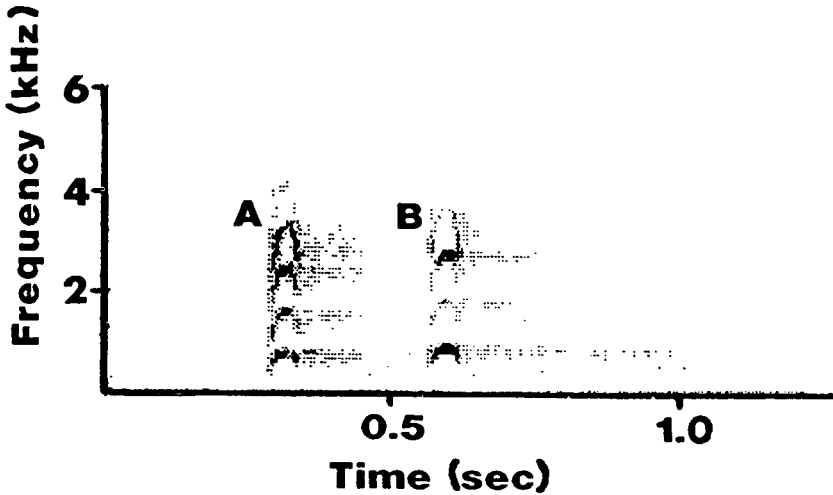


FIGURE 1. "Kik" calls by female (A) and male (B) Cooper's Hawk, recorded as the initial calls by one pair upon their arrival at the nesting area at dawn.

they themselves were building (in flight to or from the nest, from perches preparatory to collecting twigs, and/or while taking twigs; only one female gave "kik" calls [$n = 10$] and only two females gave "cak-cak-cak" calls [$n = 1-5$], but five females gave "whaaa" calls [$n = 35$ -ca. 200]). Compared to males, females thus called more frequently and had a larger repertoire of calls when in the presence of their mates. Females also called during a wider variety of activities than did males.

DISCUSSION

Other than the resident pair, Cooper's Hawks were not detected on nesting areas during the 10 episodes analyzed here (or in any of the other 76 episodes at 20 additional sites—see Methods).

Thus, we assume that the vocalizations reported have intra-pair functions. We did not hear hawks' calls from adjacent nesting areas (≥ 0.6 km apart), and females called much less frequently after males left the nesting areas, presumably to hunt.

Vocalizations may be a primary means of intra-pair communication during the pre-incubation period. Mated pairs begin their daily activities in reduced light, about 20-25 min before sunrise, with the sexes initially separated by distances averaging about 60-65 m in dense woodland vegetation where visual contact is probably difficult. Nest building typically begins soon after this brief exchange of calls, again before sunrise. Nest building by males appears to function as a pre-coital display (Rosenfield 1990), and the male's conspicuous flights to and from the nest

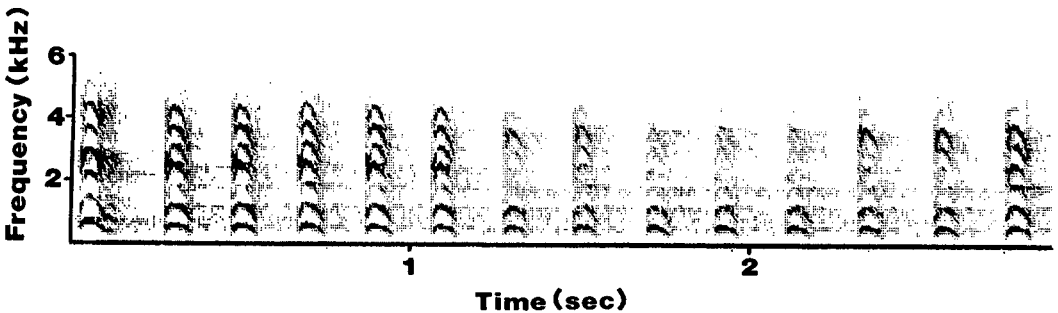


FIGURE 2. "Kik-cak-cak-cak" calls by one female Cooper's Hawk as recorded shortly after her arrival at the nesting area at dawn.

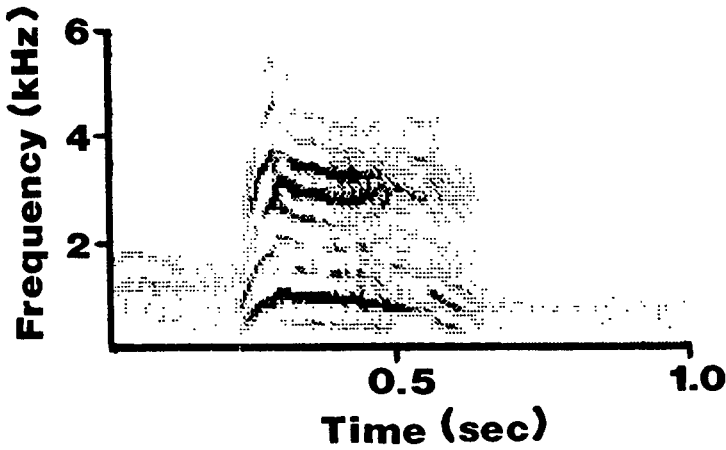


FIGURE 3. "Whaaa" call of one female Cooper's Hawk as recorded during a morning nest building bout.

(with white undertail coverts often flared) may help overcome limits on visibility in dense vegetation. However, reduced visibility at dawn may also explain why males called from the nest dur-

ing 53% ($n = 19$) of the day's first or second nest visits, but during only 1% ($n = 141$) of subsequent visits later in the morning. Taken together, dawn calls and calls in the first two nest visits

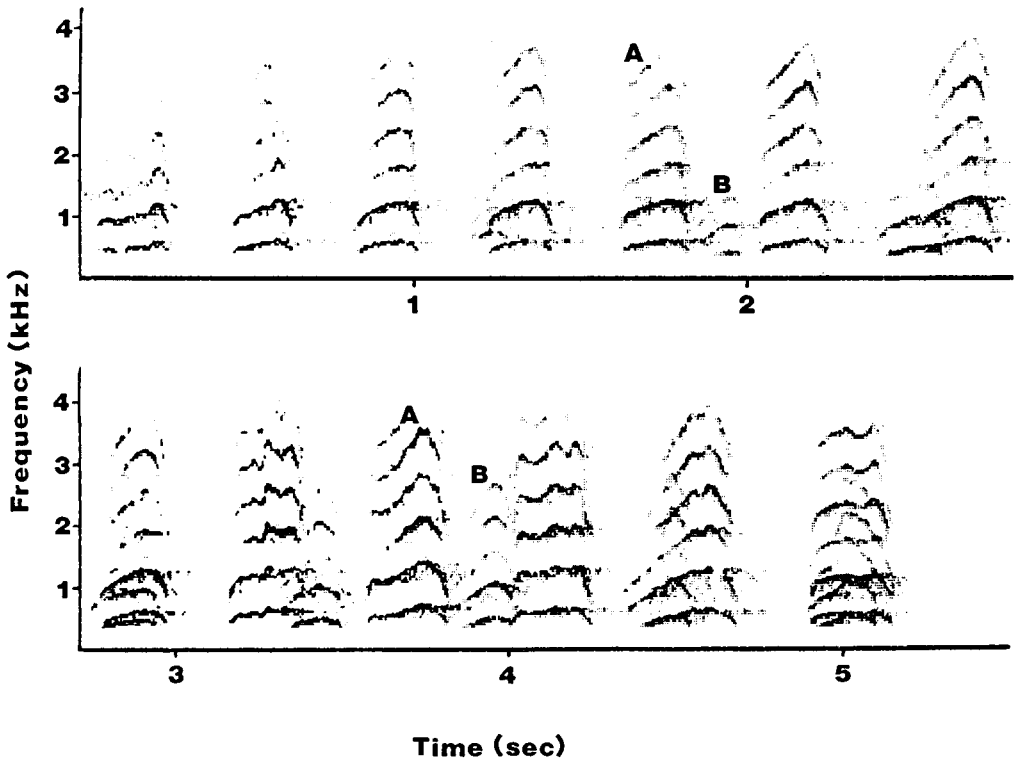


FIGURE 4. Calls of a female and male Cooper's Hawk during one copulation. Both sexes called throughout this copulation. Female notes (A) reach a maximum frequency of 4 kHz and show a longer duration than male notes (B), which have a maximum frequency of 3 kHz.

TABLE 2. Types and number of calls by female Cooper's Hawks during 10 observational episodes during pre-incubation.

Episode	Number of calls (% at dawn)		
	"kik"	"cak-cak-cak"	"whaaa"
1	12 (83)	1 (100)	121 (0)
2	14 (71)	23 (30)	83 (0)
3	27 (81)	11 (0)	81 (0)
4	10 (40)	10 (80)	0
5	2 (0)	30 (67)	0
6	0	22 (100)	60 (0)
7	5 (100)	19 (63)	486 (0.4)
8	27 (78)	58 (14)	0
9	65 (12)	32 (0)	2 (0)
10	13 (77)	3 (100)	120 (0)

accounted for a mean proportion of 95% of total male vocalizations in the episodes analyzed here.

Nevertheless, the majority of female vocalizations are given well after sunrise when the sexes are in close proximity and, compared to dawn, presumably more visible to each other. There remains a further well-marked asymmetry in vocalizations between the sexes during the pre-incubation period. Compared to males, female Cooper's Hawks (1) had a larger repertoire of calls, (2) called more frequently, and (3) called during a wider array of activities. It may be that females, compared with males, have a greater need to convey more information because they apparently control male-female interactions (Mueller 1986).

Copulation calls were given only during copulations, which were never accompanied by other types of calls in either sex. We cannot ascribe a function to these calls.

Excluding copulation calls, males uttered only "kik" calls, and these almost entirely upon arrival at nesting areas at dawn, or while visiting nests. We suggest that "kik" calls convey a male's presence and location, as well as his identity. The same "kik" call is used throughout the breeding season when males return to the nesting area with prey; regularly-used delivery sites usually lie 50–100 m from the nest (Rosenfeld and Bielefeldt, unpubl.) and incubating or brooding females are probably often unable to detect the male's arrival.

During the pre-incubation period, females also called in the same contexts (e.g., nest visits) as males, but in contrast, females also called while in flight, when changing perches, while gathering twigs, and while perched when their mates were

gathering twigs. We suggest that some female vocalizations also convey presence (they always gave "kik" and/or "cak-cak-cak" calls upon arrival at dawn) and location (males always flew to the females' perch to copulate, never the reverse). For females, calling frequently during a variety of activities may help provide more or less continuous information about her position with respect to the male. For both sexes, "kik" calls in particular seem to encode rather simple and specific locational messages from senders and equally direct meanings for receivers. We suggest, however, that females may also convey broader messages about their motivational state (i.e., dominance, submissiveness, receptiveness) through these calls.

We contend that "cak-cak-cak" calls signal aggressive intent. We heard males use them only in defending the nest against predators and intruders. Females, too, use them during nest defense, but females also use them in brief (1–7 min) exchanges of calls at dawn, perhaps to reassert their dominance (cf. Wrege and Cade 1977) on a daily basis. Excitement or alarm does not seem to be adequate alternative descriptors of the context of "cak-cak-cak" calls, because a male is likely to be excited or intensely motivated at times other than nest defense, and the female need not be alarmed at dawn.

"Whaaa" calls, given exclusively by females, are uttered occasionally when loafing on the nesting area while males are hunting (pers. observ.) and, especially, during nest building bouts when both sexes are present (Rosenfeld 1990). Six of the 10 females gave "whaaa" calls while males were building; five gave "whaaa" calls while they themselves were building. In the latter context, males tend to sit and watch silently while the female builds and calls. We suggest that the female's "whaaa" call is a non-aggressive (sensu Wrege and Cade 1977) or submissive signal of her willingness to suspend the potential for aggression and join in breeding, thereby reassuring the male that it is not dangerous to be near her. Although females occasionally displace males from perches during the pre-incubation period (pers. observ.), we have not observed overt intra-pair aggression in Cooper's Hawks at this time. This is, perhaps, one result of an effective communication system, which in this species includes intersexual differences in vocalizations.

Without experimental manipulation it is difficult to ascribe functions to behavior. This difficulty is compounded by the possibility that at

least some calls by Cooper's Hawks may be multi-functional (Lein 1980). For example, the "kik" call may simply indicate location, as proposed above, but it also is a component of a postural bowing display in Cooper's Hawks (Rosenfield and Bielefeldt 1991), where it may help males convey anti-aggressiveness or aggression-inhibiting information (sensu Wrege and Cade 1977) to the female. The "whaaa" call is given only by female Cooper's Hawks, perhaps to convey a non-aggressive motivational state. This may be analogous to the whining "female begging call" given exclusively by female Merlins (*Falco columbarius*) during the pre-incubation period. Feldsine and Oliphant (1985) suggest that female Merlins used this call to tell their mates to provide food. Female Cooper's Hawks also depend on their mates for food during the pre-laying period, as well as the entire incubation period, and part of the nesting stage. At all these stages, prey transfers are usually followed by "whaaa" calls from females.

Bird behavior is subject to multiple and potentially conflicting selective pressures (Wilson 1975) that are difficult to identify because, in part, we lack a complete understanding of a species' social system (Ficken et al. 1978). To clarify the evolution of behavior it is often advantageous to rely on comparative studies of closely related species (Lorenz 1950). Research on the vocalizations of the Sharp-shinned Hawk (*A. striatus*) at the pre-incubation stage might prove especially fruitful because this species exhibits one of the highest degrees of reversed sexual size dimorphism in raptors. As with the Cooper's Hawk, it too inhabits dense vegetation where vocalizations may also be a primary means of communication.

Our conclusions are based on observations of birds that had already undergone pair formation. Behavior during pair formation is unknown. Moreover, we did not investigate daily and seasonal variability in vocalizations of individuals and pairs. Age and previous breeding experience could influence the timing and frequency of vocalizations. For example, some postural displays may be superfluous in pairs that have previous breeding experience (Wrege and Cade 1977, Ratcliffe 1980, Rosenfield and Bielefeldt 1991) and the same might be true of vocalizations (Lein 1980). The above factors may explain the variability among individuals in our study.

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