# THE ANNUAL AND DIEL CYCLES OF GOSHAWK VOCALIZATIONS AT NEST SITES

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ABSTRACT.—I attempted to quantify seasonal and daily Northern Goshawk (*Accipiter gentilis*) vocalizations at nest sites and identify their function. Both duration and number of calls showed significant differences among different periods of the year. The daily distribution of vocalizations differed through the breeding season both as a whole and in individual stages. My results suggested that the *kek-kek* call may have two meanings as an alarm call and as a call to excite mates. During courtship, vocal activity was most intense in the early morning (female fertile period), but during other stages of the breeding season, vocal activity occurred throughout the day and was related to parental care. My results suggested that vocalizations of goshawks function primarily in territorial defense, intra-pair communication, and protection of paternity of young. Young goshawks showed a rapid increase in the duration of their total daily vocalizations within the first 10 d after fledging. Afterward their vocalization rates decreased until 40 d after fledging.

KEY WORDS: Northern Goshawk; Accipiter gentilis; annual vocal activity; daily vocal activity; functions of vocalizations.

Los ciclos de vocalizaciones diarias y anuales de Accipiter gentilis en sus sitios de anidacion

RESUMEN.—Intenté cuantificar e identificar la función de las vocalizaciones estacionales y diarias de *Accipiter gentilis* en los sitios de anidación. Tanto la duración como el número de vocalizaciones mostraron diferencias significativas entre los diferentes períodos del año. La distribución diaria de las vocalizaciones mostraron diferencias significativas entre los diferentes períodos del año. La distribución diaria de las vocalizaciones fue diferente a través de la estación reproductiva en su totalidad como por etapas individuales. Mis resultados sugieren que la vocalización del Kek-kek-kek puede tener dos significados, como señal de alarma y para atraer a la pareja. Las vocalizaciones fueron mas intensas en la mañana durante el cortejo (período fértil de la hembra) que durante las otras etapas de la actividad reproductiva, la actividad vocal durante el día estuvo mas relacionada con el cuidado parental. Mis resultados sugieren que las vocalizaciones de los azores son parte principal de la defensa del territorio, de la comunicación entre la pareja y de la protección y paternidad de los pichones. Los azores jovenes mostraron un rápido incremento en la duración total de sus vocalizaciones diarias despues de diez dias de haber emplumado, luego su tasa de vocalizaciones disminuyo a partir del día 40 despues de haber emplumado.

[Traducción de César Márquez]

Forest and woodland birds use songs to communicate in visually-obstructed habitats and contact between mates may be maintained acoustically rather than visually (Keast 1985, 1994). Vocalization patterns and their evolution have been described and quantified in passerines (Kroodsma and Miller 1996) but, for other groups of birds, the literature is not as extensive. In particular, vocalizations of raptors have rarely been quantified (Rosenfield and Bielfeldt 1991). Falconids in the genus *Herpetotheres* and *Micrastur* typically vocalize in the morning (Staicer et al. 1996) and their vocalizations may serve as greeting displays between mates (Cramp and Simmons 1980). In male Cooper's Hawks (Accipiter cooperii), there is marked vocal activity at dawn (Stewart et al. 1996) and a specific dawn call is given (Rosenfield and Bielfeldt 1991). Similar behavior has been observed in the Sparrowhawk, (Accipiter nisus) (Newton 1986).

The vocalizations of Northern Goshawks (*Accipiter gentilis*) have been described by various authors (e.g., Gromme 1935, Cramp and Simmons 1980, Squires and Reynolds 1997). These descriptions have sometimes been supplemented with remarks concerning associated behavior (Schnell 1958, Pacteau 1989). However, the vocalizations of adult and young goshawks have never been quantified. In the vocabulary of goshawks, there are two basic types of calls (Cramp and Simmons 1980, Squires and Reynolds 1997): a guttural, chattering call and a plaintive, wailing call. The chattering call has been described by Zirrer (1947), Schnell (1958), Cramp and Simmons (1980), and Squires and Reynolds (1997) as a slow *kek*... *kek*... *kek* call that is used in advertising and pair contact. There is also a fast *kek-kek-kek* call that is used as a threat and mobbing call, a subdued *kai-kai-kai* alarm call, and a soft and quick *kew-kew-kew* chattering call. Adult wailing calls (*whee-oo*... *whee-oo*) are categorized as food calls. In my analysis of adult goshawk vocalizations, I used only these major call types, because other calls are easily overlooked in the field (Penteriani unpubl. data, Squires and Reynolds 1997).

The calls of young goshawks have been described by Schnell (1958) as a *whee* ... *whee* ... *whee* food and location call, a distress call consisting of a rapid, high-pitched twitter like chickens make, a contentment call similar to the previous call but consisting of more widely-spaced, single calls, an aggressive chatter *ke-ke-ke* call used by nestlings when they have food, and a *kikk-kikk-kikk* used by nestlings to express protest or alarm.

The first objective of my study was to quantify seasonal and daily levels of goshawk vocalizations to determine if the frequency of these vocalizations varied seasonally and annually. My second objective was to determine if goshawk calls are used mainly in territorial defense, intra-pair communication (i.e., sexual attraction and sexual conflict when the presence and/or actions of one mate interfere with the adaptive interests of the other, Davies 1989), or to protect paternity. If so, I predicted that they would continue throughout the breeding season, albeit at reduced rates, and they should peak during the fertile period of females during courtship and egg laying (Birkhead and Møller 1992, Catchpole 1973, Björklund et al. 1990, Merilä and Sorjonen 1994). If vocalizations only function to attract and retain mates, then I predicted that they would occur at higher rates before incubation and cease after the start of egg laying. Because in dense habitats, such as forests, limited visual signaling leads to the development of acoustic communication, as in the case of forest passerines (Kroodsma and Miller 1996), I predicted that goshawks would spend the majority of their time vocalizing during the year and daily vocalization patterns would show similarities with song patterns of woodland passerines.

## METHODS

I noted goshawk vocalizations from 1 January 1996–31 December 1996 in a 5000-ha area of beech-forested hills of Côte d'Or (Burgundy region, France). I divided each month into three periods each consisting of 10 d. For each 10-d period and each solar day in the period, I computed the number of minutes per period and equally distributed them among eight neighboring goshawk pairs. Consequently, an hourly block was assigned to each pair on a rotation basis, and during each day of each 10-d period, I noted the vocalizations of the eight pairs. As significant changes in the breeding cycle might interfere with call data, each site was systematically monitored during the breeding period. Because each pair successfully reproduced, the annual analysis was carried out for all eight pairs selected at the start of the study.

I made observations at each nest from a location where I did not disturb the pair (about 100 m away) and I noted calls without changing my position. From these points, I also made observations concerning the behavioral context of vocalizations. This position prevented me from hearing some calls of nestlings when they were in their first few weeks of life, vocalizations of adults outside the nest stand, and vocalizations of juvenile goshawks after they left the nesting area. In each 10-d period, I recorded the time of the first and last vocalizations of the day, choosing days with minimum interference from precipitation and wind. For each type of call, I recorded the time when the call began, and its duration from a series of single calls (e.g., kek, whee-oo and whee) or call-series (e.g., kek-kek, kai-kai-kai, kew-kew-kew, and kikk-kikk-kikk). I measured the duration of the vocalizations with a stopwatch, counting the seconds elapsed from the start to the last call given <60 sec from the previous one. I assumed one minute of silence between calls or between call sequences indicated the end of a vocalization. An isolated single call received an arbitrary value of 1 sec.

Sampling units were goshawk pairs for adult vocalizations and nestlings and/or fledglings at each occupied nest for vocalizations of young. I analyzed the call data in relation to month and to the different periods of the annual breeding cycle: nonbreeding (September–January), courtship (February–March), incubation (AprI– early May), nestling period (early May–late June), and fledgling period (late June–August). If a single vocalization implied multiple call numbers, I took the average value. Only nonparametric statistics were used in the analyses (Hollander and Wolfe 1973).

#### RESULTS

Adult Vocalizations. Adult goshawk vocalizations showed one major peak during the year that coincided with the courtship period (Fig.1). The duration of the vocal events differed significantly between months (H = 73.11, P < 0.001, Kruskal-Wallis) and between periods (H = 54.86, P < 0.001). The duration of the vocal events increased during the courtship period and decreased during incubation (Table 1).

During most of the annual cycle, the first call

Table 1. Features of adult and juvenile Northern Goshawk vocal activity (N = 8) during the year. The duration (sec) represents the minimum, maximum, and average ( $\pm$ SD) call length of the monthly vocalizations by goshawks at nest sites.

	Adult Call	YOUNG CALL			
Month	DURATION (sec) min-max $(\tilde{x} \pm SD)$	DURATION (sec) min-max $(\bar{x} \pm SD)$			
			Jan	1–966	
				$159.7 \pm 194.5$	
			Feb	1-749	
$272.5 \pm 265.6$					
Mar	2-330				
	$240.7 \pm 297.2$				
Apr	2-59				
	$110.1 \pm 158.4$				
May	2-55				
	$99.7 \pm 88$				
Jun	1-112	1-1086			
	$103 \pm 130.3$	$161.5 \pm 241.5$			
Jul	2-352	1-1491			
	$85.8 \pm 77.4$	$310.9 \pm 273.6$			
Aug	4-42	1-560			
	$15.9 \pm 10$	$61.9 \pm 66.1$			
Sept	2-30				
	$12.2 \pm 5.5$				
Oct	1-128				
	$23.7 \pm 48.3$				
Nov	1-136				
	$32.2 \pm 39.1$				
Dec	0-86				
	$17.4 \pm 12.9$				

was uttered at different times of the day, except during courtship, when it was always uttered before sunrise (range = 4-45 min before sunrise). The last call was always uttered prior to sunset, except in April, when it was recorded 22 min afterwards. The last call was less related to dusk than the first call was to dawn.

During courtship, the vocalizations reached one major peak both in the first hour before sunrise and three hours after sunrise (Penteriani 1999). During incubation, nestling, and fledgling periods, the daily distribution of the vocalizations was more irregular. There was a significant difference (H =23.54, P < 0.001) in the duration of vocalizations in various hours of the day. In the nonbreeding period, the diurnal distribution of vocalizations varied and their duration was shorter. An exception was the month of January, when a peak in the same time period as in the courtship period was observed, although the duration of the vocalizations was shorter (Fig. 1). I found a difference in the day-long distribution of vocal events between courtship and incubation periods ( $D_n = 0.78$ , P < 0.001), between courtship and nestling periods ( $D_n = 0.86$ , P < 0.001), and between courtship and fledgling periods ( $D_n = 0.79$ , P < 0.001).

The chattering call kek ... kek ... kek was the most common call throughout the year (37.6%). A common pattern between the duration of the vocal events and the call number characterizing them was observed for nonbreeding ( $r_s = 0.6, P < 0.01$ , Spearman rank), courtship  $(r_{s} = 0.4, P < 0.01)$ , nestling ( $r_s = 0.46$ , P < 0.05), and fledgling periods ( $r_s = 1, P < 0.001$ ), but not for the incubation period ( $r_s = 0.24, P > 0.05$ ). The chattering call was the second most frequently-used call throughout the year (34.6%) but there was no common pattern between the duration of the vocalizations and the number of calls that characterized them in the nonbreeding ( $r_s = 0.19, P > 0.05$ ), courtship  $(r_{s} = 0.15, P > 0.05)$ , incubation  $(r_{s} = 0.29, P > 0.05)$ 0.05), nestling ( $r_s = 0.37$ , P > 0.05), and fledgling  $(r_{\rm s} = 0.08, P > 0.05)$  periods. A total of 63.2% of chattering calls were preceded and/or followed at  $\leq$ 1-min intervals by one call or a series of calls, such as pair-contact calls, food calls, and greeting calls (only once upon mating), or by an observed copulation and prey delivery. The remaining 36.8% of chattering calls were isolated vocalizations. The difference between these two situations was significant (N = 171, z = 2.86, P < 0.05, Mann-Whitney U-test).

A common pattern between the duration of vocal events and number of vocalizations characterizing the wailing call *whee-oo* . . . *whee-oo* . . . *whee-oo* (frequency = 21%) was observed for the nonbreeding ( $r_s = 0.83$ , P < 0.05), courtship ( $r_s =$ 0.46, P < 0.01), incubation ( $r_s = 0.8$ , P < 0.05), and the fledgling ( $r_s = 0.72$ , P < 0.05) periods, but not for the nestling period ( $r_s = -0.27$ , P > 0.05).

**Vocalizations of Young.** The duration of the vocal events differed between months (H = 5.76, P < 0.05), but not between nestling and fledgling periods (H = 2.16, P > 0.05). The duration of vocalizations by young goshawks during the nestling and fledgling periods increased rapidly until about the 10th day after fledging and quickly declined until about the 40th day. No vocalizations were recorded afterwards (Fig. 2).



Figure 1. Annual vocalization pattern in adult Northern Goshawks at nest sites: sum of goshawk vocal activity (sec  $\pm$  SD) per month (N = 8).

During these two periods, the time of the first call was variable, whereas the last call was always uttered before sunset. During nestling, the peaks in vocalizations occurred during the 4th and 13th hr after sunrise; conversely, during fledgling, vocalizations were clustered in the central hours of the day, between the 7th and 10th hr after sunrise. During these periods, prey delivering was related to vocal activity.

A common pattern between the duration of the vocal events and number of vocalizations characterizing the *whee*... *whee*... *whee* call (frequency = 95.1%) was observed in both the nestling ( $r_s = 0.71$ , P < 0.05) and fledgling ( $r_s = 0.78$ , P < 0.001) periods.

## DISCUSSION

My study indicated that most adult goshawk vocalizations occurred during the courtship period. Most vocalizations occurred in late winter and early spring, prior to breeding and corresponded to initial courtship and territory establishment. Various studies of Northern Hemisphere birds have made similar observations (e.g., Kelsey 1989, Logan et al. 1990, Catchpole and Slater 1995). It was noteworthy that the types of calls recorded from January onwards (about 3 mo before egg laying) were similar to those recorded during courtship. Starting in January, goshawks begin to become more territorial and they utter their alarm calls when people walk close to their nests. They are regularly observed displaying over nesting territories and woods (Anonymous 1990, Toyne 1997). Goshawks also intensified their vocalizations at the end of their reproductive cycle when young were dispersing from nest areas. The sole period when no vocalizations were recorded near nests was from late November to the first 20 d of December. A comparison of the durations and numbers of calls given showed a similar pattern during the year with the period with the longest and most numerous vocalizations coinciding with the courtship period. Overall, the greatest number of daily vocalizations, the longest series of calls, and the most complex individual calls within each series of calls occurred during the courtship period.

During the courtship period, vocalizations were clustered from 1 hr before sunrise through the



PENTERIANI

Figure 2. Vocalization pattern in juvenile Northern Goshawks during the nestling and fledgling periods (from June to August).

three following hours and the first call was always uttered prior to sunrise. This finding was pertinent to the survey methodologies currently being used to locate goshawk nests (Penteriani 1999). This time period also corresponded to the daily copulation pattern of adults with a peak occurring around the time of egg laying early in the morning and when male goshawks spend most of their time near females (Møller 1987).

The second peak in goshawk vocalizations during the breeding cycle might be ascribed to the intense activity of goshawks near their nests during the nestling period. The third and less intense peak during fall might be dependent on levels of gonadal hormones which are responsible for the activation of song behavior in most adult birds (Nottebohm et al. 1978, Brenowitz and Kroodsma 1996). Elevated levels of hormones might also be a nonfunctional cause of the singing peak at dawn (Staicer et al. 1996).

The high frequency of the *kek-kek* alarm call during the courtship period indicated that the meaning so far attributed to this call (e.g., Kimmel and Yahner 1990, Speiser and Bosakowski 1991, Kennedy and Stahlecker 1993) should not be confined to threat and mobbing, at least near the nest. The fact that up to 60% of these calls were always preceded and/or followed by pair contact, food, and greeting calls strongly supported this function. Nevertheless, I attributed a twofold meaning to this call related to alarm and high excitement during mate contacts. In most cases, this chattering call followed a series of kek . . . kek . . . kek or pair-contact calls, especially during territory establishment and until egg laying. Therefore, it was not necessarily related to stress or defense but also to breeding period. In a species, the same call may be uttered in different contexts, including conspecific territorial fights, defense against predators, and intra-pair interactions without the presence of any predator or territorial competitor (Logan 1994). It should also be emphasized that, during the reproductive season, aggressive calls may also express sexual conflicts (Davies 1989).

Vol. 35. No. 1

I considered the *whee-oo* ... *whee-oo* ... *whee-oo* call to be an exclusive female food call. During the incubation period, it was given by females when food deliveries were made by males (Schnell 1958)

and it denoted a very important stage in the breeding activity of the pair. In fact, during incubation and nestling (Schnell 1958, Penteriani unpubl. data), females utter this call as soon as they see or hear males in the nest area (recognition scream), upon prey delivery (transfer scream), and if males remain in the nest area after food delivery (dismissal scream). During the fledgling period, this call might be part of the communication between females and young when females continue to feed young after fledgling (Schnell 1958).

The vocalizations of young at nests increased from hatching until the first 10 d after they fledged. After that, vocalizations diminished and ended about 40 d after the young first left nests or approximately 80 d after hatching when dispersal from nesting areas typically occurs (Kenward et al. 1993a). This decrease in vocalizations after fledging may have been due to the fact that, before dispersing, juveniles can fly as far as 1 km from nests (Kenward et al. 1993b). Since the whee . . . whee . . . whee call of young goshawks is mainly interpreted as a food call, the day-long pattern I observed suggested that adults continued to make food deliveries to nests. Although food may be supplied to nestlings at all times of the day (Schnell 1958), peaks in vocalizations by young in my study, as well as the changes observed between the nestling and fledgling periods, fit the peaks reported by Schnell (1958) for food deliveries by male goshawks (74-85% of total food deliveries).

The day-long and annual patterns of goshawk vocalizations suggested that the vocal activity in goshawks functions primarily in territorial defense and intra-pair communication. This finding was supported by the fact that vocalizations continued throughout the breeding season and the year, albeit at different rates. Moreover, as vocalizations showed a peak during the fertile period of females, it also seemed that calls may be used to protect paternity.

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#### LITERATURE CITED

ANONYMOUS. 1990. Breeding biology of goshawks in lowland Britain. *Brit. Birds* 83:527–540.

- BIRKHEAD, T. AND A.P. MØLLER. 1992. Sperm competition in birds. Evolutionary causes and consequences. Academic Press, Cambridge, U.K.
- BJÖRKLUND, M., B. WESTMAN, AND K. ALLANDER. 1990 Song in Swedish Great Tits: intra- or intersexual communication? *Behaviour* 111:257–269.
- BRENOWITZ, E.A. AND D.E. KROODSMA. 1996. The neuroethology of birdsong. Pages 285–304 in D.E. Kroodsma and E.H. Miller [EDS.], Ecology and evolution of acoustic communication in birds. Cornell Univ. Press, Ithaca, NY U.S.A.
- CATCHPOLE, C.K. 1973. The functions of the advertising song in the Sedge Warbler (*Acrocephalus schoenobaenus*) and the Reed Warbler (*A. scirpaceus*). *Behaviour* 46:300–320.
- CRAMP, S. AND K.E.L. SIMMONS. 1980. Handbook of the birds of Europe, the Middle East and North Africa Vol. 2. Oxford Univ. Press, Oxford, U.K.
- DAVIES, N.B. 1989. Sexual conflict and the polygamy threshold. Anim. Behav. 38:226-234.
- GROMME, O.J. 1935. The goshawk (Astur atricapillus atricapillus) nesting in Wisconsin. Auk 52:15–20.
- HOLLANDER, M. AND D.A. WOLFE. 1973. Nonparametric statistical methods. Wiley, New York, NY U.S.A.
- KEAST, A. 1985. Springtime song, periodicity and sequencing, a comparison of a southern forest and northern woodland bird community. Pages 119–128 in A. Keast, H.F. Recher, H. Ford, and D. Saunders [EDS.], Birds of eucalyptus forests and woodlandsecology, conservation, management. RAOU and Surrey Beatty and Sons, Sydney, Australia.
- ——. 1994. The annual cycle in a vocalization context a comparison of the Eastern Yellow Robin Eopsaltria australis and Jacky Winter Microeca leucophaea. Emu 94: 230–238.
- KELSEY, M.B. 1989. A comparison of the song and territorial behavior of a long-distance migrant, the Marsh Warbler Acrocephalus palustris, in summer and winter *Ibis* 131:403–414.
- KENNEDY, P.L. AND D.W. STAHLECKER. 1993. Responsiveness of nesting Northern Goshawks to taped broadcasts of three conspecific calls. J. Wildl. Manage. 57. 249–257.
- KENWARD, R.E., V. MARCSTROM, AND M. KARLBOM. 1993a. Post-nestling behaviour in goshawk, *Accipiter gentilis*: I The causes of dispersal. *Anim. Behav.* 46:365–370.
- , \_\_\_\_\_, AND \_\_\_\_\_. 1993b. Post-nestling behaviour in goshawk, Accipiter gentilis: II. Sex differences in sociality and nest-switching. Anim. Behav. 46:371–378.
- KIMMEL, J.T. AND R.H. YAHNER. 1990. Response of Northern Goshawks to taped conspecific and Great Horned Owl calls. *J. Raptor Res.* 24:107–112.
- KROODSMA, D.E. AND E.H. MILLER. 1996. Ecology and evo-

lution of acoustic communication in birds. Cornell Univ. Press, Ithaca, NY U.S.A.

- LOGAN, C. 1994. Fluctuations in intra-pair calling across breeding phases in Northern Mockingbirds (*Mimus polyglottos*). *Behaviour* 130:123–141.
- —, L.L. HYATT, AND L. GREGORCYK. 1990. Song playback initiates nest building during clutch overlap in Mockingbirds *Mimus polyglottus*. Anim. Behav. 39:943– 953.
- MERILÄ, J. AND J. SORJONEN. 1994. Seasonal and diurnal patterns of singing and song-flight activity in Bluethroats (*Luscinia svecica*). Auk 111:556–562.
- Møller, A.P. 1987. Copulation behaviour in the goshawk Accipiter gentilis. Anim. Behav. 35:755–763.
- NEWTON, I. 1986. The Sparrowhawk. T. & A.D. Poyser, Staffordshire, U.K.
- NOTTEBOHM, F., M.E. NOTTEBOHM, L.A. CRANE, AND J.C. WINGFIELD. 1978. Seasonal changes in gonadal hormone levels of adult male canaries and their relation to song. *Behav. Neural Biol.* 47:197–211.
- PACTEAU, C. 1989. L'autour et l'épervier, du comportement au sujet. Editions Hécate, Luçon, France.
- PENTERIANI, V. 1999. Dawn and morning goshawk courtship vocalizations as a method for detecting nest sites. J. Wildl. Manage. 63:511–516.
- ROSENFIELD, R.N. AND J. BIELFELDT. 1991. Vocalizations of Cooper's Hawks during the pre-incubation stage. *Condor* 93:659–665.

- SCHNELL, J.H. 1958. Nesting behavior and food habits of goshawks in the Sierra Nevada of California. *Condor* 60:377–403.
- SPEISER, R. AND T. BOSAKOWSKI. 1991. Nesting phenology, site fidelity, and defense behavior of Northern Goshawk in New York and New Jersey. J. Raptor Res. 25. 132–135.
- SQUIRES, J.R. AND R.T. REYNOLDS. 1997. Northern Goshawk (*Accipiter gentilis*). In A. Poole and F. Gill [EDS], The birds of North America, No. 298. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC U.S.A.
- STAICER, C.A., D.A. SPECTOR, AND A.G. HORN. 1996. The dawn chorus and other diel patterns in acoustic signaling. Pages 426–453 in D.E. Kroodsma and E.H Miller [EDS.], Ecology and evolution of acoustic communication in birds. Cornell Univ. Press, Ithaca, NY U.S.A.
- STEWART, A.C., R.W. CAMPBELL, AND S. DICKIN. 1996. Use of dawn vocalizations for detecting breeding Cooper's Hawks in an urban environment. *Wildl. Soc. Bull.* 24 291–293.
- TOYNE, E.P. 1997. Nesting chronology of Northern Goshawks (*Accipiter gentilis*) in Wales: implications for forest management. *Forestry* 70:121–127.
- ZIRRER, F. 1947. The goshawk. Passenger Pigeon 9:79-94

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