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RESEARCH ARTICLE

Vocal Activity of Lesser Galagos (*Galago* spp.) at Zoos

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Almost nothing is known about the natural vocal behavior of lesser galagos living in zoos. This is perhaps because they are usually kept in nocturnal exhibits separated from the visitors by a transparent and acoustically insulating glass barrier. The aim of the present study was therefore to fill this gap in knowledge of the vocal behavior of lesser galagos from zoos. This knowledge might be beneficial because the vocalizations of these small primates can be used for species determination. We performed a 10-day-long acoustic monitoring of vocal activity in each of seven various groups of *Galago senegalensis* and *G. moholi* living at four zoos. We quantitatively evaluated the occurrence of four loud vocalization types present in both species, including the most species-specific advertisement call. We found that qualitative as well as quantitative differences exist in the vocal behavior of the studied groups. We confirmed that the observed vocalization types can be collected from lesser galagos living at zoos, and the success can be increased by selecting larger and more diverse groups. We found two distinct patterns of diel vocal activity in the most vocally active groups. *G. senegalensis* groups were most vocally active at the beginning and at the end of their activity period, whereas one *G. moholi* group showed an opposite pattern. The latter is surprising, as it is generally accepted that lesser galagos emit advertisement calls especially at dawn and dusk, i.e., at the beginning and at the end of their diel activity. Zoo Biol. XX:XX–XX, 2016.

Keywords: acoustic monitoring; Galagidae; *Galago moholi*; *Galago senegalensis*; species-specific vocalizations

INTRODUCTION

Due to their nocturnal activity and small body size, lesser galagos (*Galago* spp.) at zoos are usually housed in nocturnal exhibits separated from the public area by a transparent and acoustically insulating glass barrier [Brandl, 2014]. Therefore, their vocal displays seem to remain much more hidden from zoo staff and visitors in comparison to the larger and diurnal primates that are kept in acoustically uninsulated exhibits. Therefore, little is known about the natural vocal behavior of lesser galagos in zoos. Filling this gap in our knowledge might be beneficial for further breeding management of these small primates at zoos. First,

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several studies have noted the importance of using natural vocal behavior in evaluations of welfare of captive animals [Ruiz-Miranda et al., 1998; Boinski et al., 1999]. Second, and probably more importantly, the vocal behavior of the whole Galagidae family has shown to be highly applicable to taxonomy and species determination [Zimmermann et al., 1988; Zimmermann, 1990; Anderson et al., 2009; Bearder et al., 2013].

Lesser galagos include four extant species that are widespread in sub-Saharan Africa [Butynski et al., 2013]. They show a lack of overt morphological diversity, which, together with the still unresolved taxonomy of the genus and the whole Galagidae family [Kingdon, 1997; Butynski et al., 2013; Pozzi et al., 2014], complicates their correct determination and thus their breeding management at zoos. Previously, some of their vocalizations, especially the advertisement call, have been demonstrated to significantly contribute to species determination [Zimmermann et al., 1988; Zimmermann, 1990]. However, vocal behavior has never been taken into account when determining the species of lesser galagos at European zoos. Instead, the location of capture of the founding animals has been the prevailing cue used by zoo managers for species determination of their lesser galagos. In the European Association of Zoos and Aquaria (EAZA) member zoos, groups established from founders captured in Guinea, Ghana, and Togo were presumed to be the Senegal lesser galago, *Galago senegalensis*; these galagos have been kept separately from those established from founders captured in Botswana and also from those of unknown origin that are presumed to be the South African lesser galago, *G. moholi*.

Recently, genetic screening was launched to verify the accuracy of the presumed species determination of the lesser galagos living at European zoos [Brandl, 2014], and the hesitation to use vocal behavior still remains. This is understandable because the experience with natural vocal behavior of these animals is highly limited at zoos for the reasons that are noted above. Furthermore, lesser galagos living at zoos could indeed show decreased vocal activity because they are often kept as a single family group or even just as a pair without acoustic or any other contact with other groups. Bearder et al. [2013] stated that the need for the advertisement call can be reduced in a wild group of few individuals occurring in an isolated patch of forest. Farmer et al. [2011] reported lower or zero howl rates in groups of captive howler monkeys (*Alouatta caraya*) that contained fewer members and had no auditory access to other groups. Captive animals may also change their behavior, including decreasing vocal activity, as a consequence of environmental disturbances [Castellote and Fossa, 2006]. Noise emerging from the viewing public also has a significant effect on the behavior of zoo animals [Owen et al., 2014; Quadros et al., 2014; Larsen et al. 2015]. Therefore, the first aim of our study was to investigate the natural vocal behavior of lesser galagos living at zoos, specifically to examine whether they spontaneously produce vocalizations that potentially can be used for species determination. For this purpose, we performed 10-day-long acoustic monitoring of vocal activity in each of seven various groups of *G. senegalensis* and *G. moholi* living at four zoos. Although the vocal repertoire of the lesser galagos includes more types of homologous species-specific vocalizations [Zimmermann, 1985; Zimmermann et al., 1988], we have selected and quantitatively evaluated the occurrence of four loud species-specific vocalization types (Table 1). These vocalization types encompassed all behavioral categories in which vocalizations could be produced by the lesser galagos, the contact, attention/alarm, and agonistic category [Zimmermann, 1985; Zimmermann et al., 1988].

The collection of species-specific vocalizations can be significantly streamlined at zoos if the time of the highest vocal activity of the animals is known. In the lesser galagos, production of the most diagnostic advertisement call, which is probably used for long-distance spacing between conspecifics, is reported to be particularly high at dawn and dusk [Bearder et al., 2003]. However, only limited data that specifically address this issue have been published to date for wild, as well as captive, populations. Therefore, we also focused on the diel vocal activity patterns of the observed groups in the present study.

METHODS

Study Groups

Acoustic monitoring was performed in four groups of lesser galagos previously determined to be *G. senegalensis*, which were housed at four European zoos, including the Prague Zoo, Czech Republic [www.zoopraha.cz/en]; the Ostrava Zoo, Czech Republic [www.zoo-ostrava.cz/en/]; the Zoo and Botanical Garden Plzeň, Czech Republic [www.zooplzen.cz/en/]; and the Dierenpark Amersfoort, Netherlands [www.dierenparkamersfoort.nl/], and in three groups of lesser galagos previously determined to be *G. moholi*, which were housed at the Prague Zoo, Czech Republic. In the case of *G. senegalensis*, groups differed in size and composition, comprising different individuals, whereas in the case of *G. moholi*, the groups differed in size and composition but overlapped in individual membership. Table 2 summarizes all study groups and information on their size and composition as well as on their home zoos.

Housing Conditions

The housing of the study groups differed. Some groups were housed in exhibits, whereas others were housed off-exhibit. Some groups were under a reversed 12-hr day/night cycle (only *G. senegalensis* group from the Prague Zoo was under a reversed 14/10-hr day/night cycle), whereas others were under a normal 12-hr day/light cycle. These housing conditions were to some extent related to some groups being exposed to minimal interference by visitors and zoo staff, whereas other groups were exposed to higher interference by

TABLE 1. Four loud vocalization types homologous for *Galago senegalensis* and *G. moholi* and observed in the present study

Vocalization type				
G. senegalensis	*G. moholi*	Behavioral context	Description	References
Woo 1	Bark	Contact	The most diagnostic vocalization type, also referred to as an advertisement or loud call. Consists of several single (*G. senegalensis*), double or triple (*G. moholi*) notes of tonal structure. Emitted by both males and females. Significantly contributes to discrimination between *G. senegalensis* and *G. moholi*, which had been considered conspecifics until the end of the 1980s	Zimmermann [1985,1990]; Zimmermann et al. [1988]; Anderson et al., [2000]
Fwa	Yap	Attention/alarm	Less species-specific vocalization type that still allows reliable species discrimination. Predominantly noisy acoustic structure. Emitted by both males and females	Zimmermann [1985,1990]; Zimmermann et al. [1988]; Anderson et al., [2000]
Tjong	Moan	Attention/alarm	Less species-specific vocalization type that still allows reliable species discrimination. Noisy or tonal acoustic structure. Emitted by both males and females	Zimmermann [1985,1990]; Zimmermann et al. [1988]; Anderson et al., [2000]
Wik	Chatter	Agonistic	One of the least species-specific vocalization types in the lesser galagos' vocal repertoire. Harmonic structure often superimposed by noise. Emitted by both males and females	Zimmermann [1985,1990]; Zimmermann et al. [1988]

visitors and zoo staff. Some groups also shared their exhibits or off-exhibit rooms with other species of animals. As for feeding, all groups were fed before or at the beginning of their activity period. Table 2 provides detailed information on the housing conditions for each study group.

Acoustic Monitoring

Acoustic monitoring at the zoos was carried out during the years 2013 and 2014. The vocal activity of each study group was monitored for 10 consecutive days, once during the 2-year study period. For this purpose, we used the automated audio recorder Song meter SM2+ (Wildlife Acoustics, Concord, Massachusetts), which is designed for scheduled recording of wildlife vocalizations. The recorder is fully autonomous and therefore enabled collection of the vocalizations with minimal disturbances to the animals. The recorder was either placed at a suitable place outside the off-exhibit cages or was protected by wire mesh and allowed to hang from a branch inside the galagos' enclosures in the exhibits. To habituate the animals to its presence, we usually placed the recorder in the off-exhibit rooms or in the exhibits minimally 1 day in advance of the 10-day-long acoustic monitoring. In each group, the recorder was programmed to record vocalizations daily for 12 consecutive hours in concordance with the night period of its day/night cycle, i.e., concordant with the active period of the group. Table 2 provides detailed information on the acoustic monitoring in each group, specifically on the months and days in which the acoustic monitoring was performed, and the diel time schedule programmed.

Evaluation of Vocal Activity

The recordings were analyzed using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany). We performed one-zero sampling [Martin and Bateson, 2007] for each of the four predefined loud vocalization types that were homologous in the studied species ("woo1/bark," "fwa/yap," "tjong/moan," and "wik/chatter"). These loud vocalization types were identified on the basis of our preliminary observations [Schneiderová et al., 2014], comparison with previously published descriptions and spectrograms [Zimmermann, 1985; Zimmermann et al., 1988], and comparison with freely available recordings [Bearder et al., 2013]. These four loud vocalization types included all the three previously defined main behavioral categories: the contact ("woo1/bark"), attention/alarm ("fwa/yap" and "tjong/moan"), and agonistic ("wik/chatter") categories [Zimmermann, 1985; Zimmermann et al., 1988].

To perform one-zero sampling, we divided the recordings into 30-min intervals; that is, each day consisted of 24 intervals. Loud vocalization types were emitted infrequently by the lesser galagos, but when these vocalizations occurred, they could be emitted repeatedly in long series lasting for several minutes where single vocalizations were not distinctly separated from each other. Thus, we

TABLE 2. Detailed information on study groups of the lesser galagos, including their identity, home zoo, location, size and composition, housing conditions, and the acoustic monitoring performed

Study group			Housing conditions					Acoustic monitoring	
No.	Species	Zoo	Location[a]	Composition[b]	Night cycle	Staff/public activity[c]	Other species[d]	Monitoring days	Time schedule
[1]	*G. senegalensis*	Prague	Exhibit	5,4,4	9 am–7 pm	9 am–6 pm	*Pedetes capensis*	May 5–14, 2013	9 am–9 pm
[2]	*G. senegalensis*	Ostrava	Exhibit	1,3,1	9 am–9 pm	9 am–7 pm		May 22–31, 2013	9 am–9 pm
[3]	*G. senegalensis*	Plzeň	Exhibit	1,1	9 am–9 pm	8 am–7 pm	*Atherurus africanus* *Rousettus aegyptiacus*	September 20–29, 2013	9 am–9 pm
[4]	*G. senegalensis*	Amersfoort	Off-exhibit	0,2 2,0 1,1,2	10 am–10 pm	8 am–4 pm	*Echinops telfairi* *Nycticebus pygmaeus*	December 17–26, 2013	10 am–10 pm
[5]	*G. moholi*	Prague	Exhibit	1,1[e]	7 pm–7 am	9 am–6 pm	*Atherurus africanus*	August 25–28, 2013 September 5–10, 2013	7 pm–7 am
[6]	*G. moholi*	Prague	Off-exhibit	1,0 1,0 2,0 0,2	7 pm–7 am	 7–9 am 3–4 pm	various bird species housed in the neighboring room	February 15–25, 2014	7 pm–7 am
[7]	*G. moholi*	Prague	Off-exhibit	2,0[e]	7 pm–7 am	7–9 am 3–4 pm		March 31, 2014 April 1–9, 2014	7 pm–7 am

[a]Housed either as a group of more individuals in an exhibit (group composition stated in a single line), or as singles, pairs or small families in separate off-exhibit cages, but, with at least acoustic contact maintained with each other (group composition stated in several lines, each line states residents of one cage).
[b]Stated as male, female, undetermined juvenile.
[c]Opening hours of the pavilion are stated in the case of exhibits, working hours of the zoo staff are stated in the off-exhibit case.
[d]Other species sharing a common exhibit, or housed in separate off-exhibit cages.
[e]These individuals were a part of the group 6 at the time when the acoustic monitoring was performed in this group.

considered 30 min as an appropriate length of the sample interval to assess reliably the occurrence of each loud vocalization type emitted by each group. With 10 days of recordings, we obtained 240 intervals for each study group. In each interval, we scored "1" (positive score) if the vocalization type was observed and "0" (negative score) if it was not. The occurrence of each vocalization type was then expressed as the proportion of all sample intervals in which it was positively scored [Martin and Bateson, 2007]. Using this method, we obtained comparable data for all studied groups: specifically, which vocalization types were uttered, how often, and when during the activity period.

All recordings were manually analyzed by the same observer. That is, spectrograms of all the recordings were visually checked for observed vocalizations, and suspicious sounds were considered to definitely confirm or deny that they represented the observed vocalizations. We observed the loudest vocalization types in the lesser galagos' vocal repertoire; thus, they could be noticed easily and reliably in a large amount of recordings. Despite its disadvantages regarding possible bias in measurements, one-zero sampling provides high inter- and intra-observer reliability [Martin and Bateson, 2007].

Data Analysis

For each group, we calculated the average proportion of intervals with at least one positively scored vocalization type. Then, we calculated the total number of positive scores for each group and the proportion of each vocalization type within this total number. In addition, we also calculated the total number of positive scores for each vocalization type and the relative contribution of each study group to this total number. The data violated the assumption of independence of samples (in the case of the *G. moholi* groups) and would have required pooling of the highly variable samples (*G. moholi* and *G. senegalensis*) for the application of inferential statistics. Following Kuhar [2006], we were able to avoid such a procedure, preferring to provide descriptive and graphical presentation of the results.

We only report one formal statistical test, which was performed separately for each group in Stata 13 (StataCorp LP, College Station, TX). We tested for differences in the diel vocal activity in each group. For this, we divided the 12 hr of observed vocal activity on each recording day into six 2-hr periods, where each period comprised four 30-min intervals. These six periods were compared statistically by Pearson's χ^2 test for independence. To obtain the frequency table for this statistical test, we cross-tabulated the periods with the 1–0 scores from the individual intervals from all ten days of the recording.

RESULTS

Representative spectrograms of all types of the vocalizations recorded for our study groups are presented in Figure 1. The average proportion of intervals with at least one positively scored vocalization type ranged from 0.8% in the *G. moholi* group containing two males [group 7] to 61.7% in the larger *G. moholi* group housed off-exhibit [6] (Fig. 2).

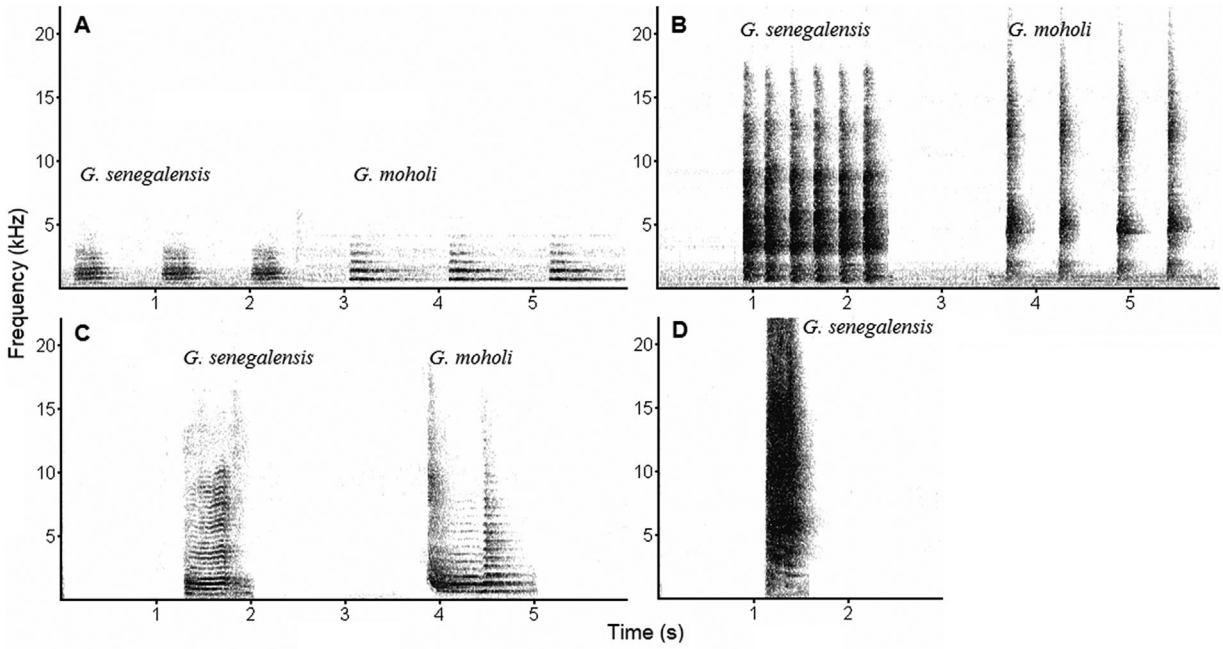

Fig. 1. Representative spectrograms of homologous vocalization types recorded from studied groups of *Galago senegalensis* and *G. moholi*. (**A**) "woo1/bark" contact vocalization, (**B**) "fwa/yap" attention/alarm vocalization, (**C**) "tjong/moan" attention/alarm vocalization, and (**D**) "wik" agonistic vocalization. The agonistic vocalization "chatter" was not recorded from any of the studied groups of *G. moholi*; thus, is not shown in this figure. Spectrogram parameters: FFT length 512, Hamming window, frame size 100%, overlap 0%.

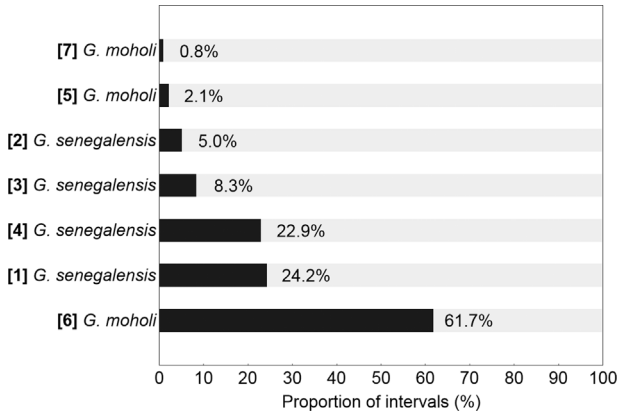

Fig. 2. Average proportion of intervals in percentages with at least one positively scored vocalization type. The most vocally active groups were the larger and more diverse groups, whereas groups containing only two individuals showed lower vocal activity.

The four observed vocalization types were not recorded from all the studied groups. Groups containing only two members [3, 5, and 7] emitted a maximum of two vocalization types, whereas the rest of the groups emitted at least three vocalization types (Fig. 3). The "tjong/moan" attention/alarm vocalization and the "wik/chatter" agonistic vocalization were not observed in any of the groups containing only two members [3, 5, and 7]. The "woo1/bark" advertisement call was not observed in two *G. moholi* groups containing only two members [5 and 7]. In the remaining groups, the relative occurrence of this vocalization type, which is the most diagnostic, ranged from 20% to 98% of the total positive scores (Fig. 3). The most commonly emitted vocalization type in the sense that it was observed in all the studied groups was the "fwa/yap" attention/alarm vocalization. Its relative occurrence ranged from 1% to 100% of the total positive scores (Fig. 3).

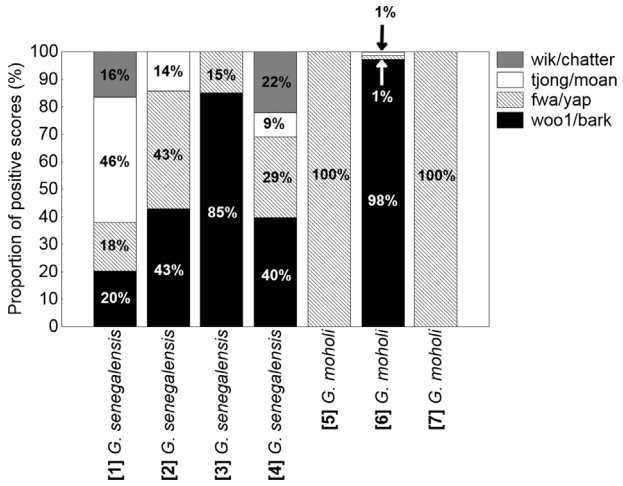

Fig. 3. Proportion of positive scores of each of four observed vocalization types from the total number of positive scores in each studied group. Groups containing only two members emitted a maximum of two vocalizations types, whereas the rest of the groups emitted at least three vocalization types. The "fwa/yap" attention/alarm vocalization was the most commonly emitted vocalization type in that it was observed in all the studied groups. The "wik/chatter" agonistic vocalization was the rarest vocalization type and was observed in only two groups.

The relative contributions of the studied groups to each of the four observed vocalization types are shown in Figure 4. The pronouncedly highest contribution to the total number of positive scores for the "woo1/bark" advertisement call, which is the most diagnostic, was observed in the larger *G. moholi* group housed off-exhibit [6]. The highest contribution to the total number of positive scores for the "fwa/yap" attention/alarm vocalization type was observed in two *G. senegalensis* groups from Amersfoort [4] and Prague [1]. The pronouncedly highest contribution to positive scores for the "tjong/moan" attention/alarm vocalization was observed in the *G. senegalensis* group from Prague [1]. The "wik/chatter" agonistic vocalization was almost evenly positively scored only for the *G. senegalensis* groups from Amersfoort [4] and from Prague [1].

We found significantly unequal diel distribution of the overall vocal activity only in the three most vocally active groups [1, 4, and 6] (Table 3; Fig. 5). The *G. senegalensis* groups from Prague [1] and Amersfoort [4] showed the highest vocal activity at the beginning and at the end of their diel activity, whereas the larger *G. moholi* group housed

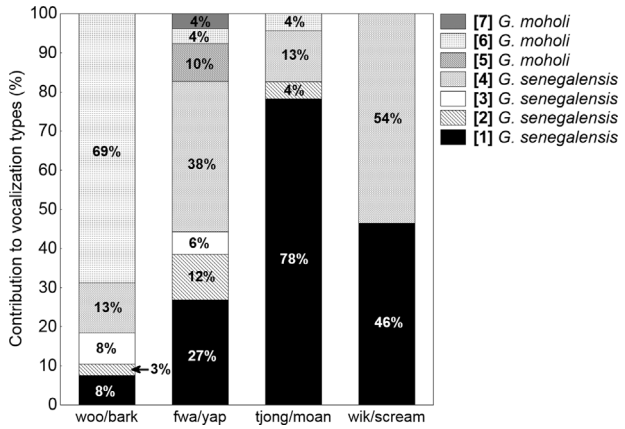

Fig. 4. Contribution of each studied group to the total number of positive scores for each of the four observed vocalization types. The highest contribution to the "woo1/bark" advertisement call, which was the most diagnostic, was observed in the larger groups housed off-exhibit where singles, pairs, or small family groups were housed in separate cages but maintained at least acoustic contact with each other. The highest contribution to the "fwa/yap" attention/alarm vocalization was observed in two larger groups that could be potentially disturbed by the presence of visitors, zoo staff, and other animals sharing their exhibits. Additionally, there was more than one male housed in a common area in these groups. The highest contribution to the "tjong/moan" attention/alarm vocalization was observed in a larger group, where five adult males were housed in a common area. The "wik/chatter" agonistic vocalization was almost evenly produced by two groups where disputes, especially between adult males, could be expected on the basis of the group composition.

TABLE 3. Results of Pearson's χ^2 test testing differences in diel distribution of overall vocal activity, and of each vocalization type observed separately

Group	All vocalization types		"Woo1/bark"		"Fwa/yap"		"Tjong/moan"		"Wik/chatter"	
	χ^2 (*d.f.* = 5)	*P*	χ^2 (*d.f.* = 5)	*P*	χ^2 (*d.f.* = 5)	*P*	χ^2 (*d.f.* = 5)	*P*	χ^2 (*d.f.* = 5)	*P*
[1] *G. senegalensis*	11.64	<0.05	3.75	0.59	6.98	0.22	9.80	0.08	22.85	<0.001
[2] *G. senegalensis*	4.21	0.52	6.15	0.29	2.05	0.84	4.03	0.55	–	–
[3] *G. senegalensis*	10.91	0.05	16.27	<0.05	7.09	0.21	–	–	–	–
[4] *G. senegalensis*	12.57	<0.05	13.40	<0.05	5.02	0.41	12.31	<0.05	11.73	<0.05
[5] *G. moholi*	3.47	0.63	–	–	3.47	0.63	–	–	–	–
[6] *G. moholi*	36.52	<0.001	33.51	<0.001	10.08	0.07	10.08	0.07	–	–
[7] *G. moholi*	10.08	0.07	–	–	10.08	0.07	–	–	–	–

Missing values indicate that the test could not be performed because the vocalization types were not emitted by the groups.

off-exhibit [6] showed an opposite pattern (Fig. 5). These patterns of vocal activity to some extent corresponded to patterns observed for the "woo1/bark" advertisement call separately (Fig. 6). However, significant differences in the diel production of this vocalization type were found only in the case of the *G. senegalensis* group from Amersfoort [4] ($\chi^2 = 13.40$; $d.f. = 5$; $P < 0.05$) and the larger *G. moholi* group housed off-exhibit [6] ($\chi^2 = 33.51$; $d.f. = 5$; $P < 0.001$). A significantly unequal diel distribution of the advertisement call was additionally found in the *G. senegalensis* group from Plzeň [3] ($\chi^2 = 16.27$; $d.f. = 5$; $P < 0.01$). We did not find any differences in the diel production of the "fwa/yap" attention/alarm vocalization, but we found significant differences in the diel production of the "tjong/moan" attention/alarm vocalization in the *G. senegalensis* group from Amersfoort [4] ($\chi^2 = 12.31$; $d.f. = 5$; $P < 0.05$). We also found significant differences in the diel production of the "wik/chatter" agonistic vocalization in both *G. senegalensis* groups that produced it: the group from Prague [1] ($\chi^2 = 22.85$; $d.f. = 5$; $P < 0.001$), as well as from Amersfoort [4] ($\chi^2 = 11.73$; $d.f. = 5$; $P < 0.05$).

DISCUSSION

We used a methodological approach that was primarily designed for wildlife recording and monitoring to investigate the natural vocal behavior of lesser galagos living under zoo conditions. We focused on the production of four loud vocalization types encompassing three main behavioral categories: contact, attention/alarm, and agonistic [Zimmermann, 1985; Zimmermann et al., 1988]. Although these vocalization types often remain unnoticed by zoo staff and visitors, we can conclude, based on our results, that lesser galagos utter them spontaneously and regularly. We also found that these vocalization types probably could be heard more frequently from larger and more diverse groups. Such groups were more vocally active in that they emitted more vocalization types and provided positive scores more often for these vocalization types. This result is not surprising because individuals from such groups are assumed to face more frequent and varied interactions with other group members and thus have an increased need to communicate.

The most frequent vocalization type in that it was emitted by all the studied groups was the "fwa/yap" attention/alarm vocalization. This corresponds to observations on other primate species, especially the brown capuchin (*Cebus apella*), in which the alarm vocalization type also represents one of the most common vocalizations encountered under captive conditions [Boinski et al., 1999]. Zimmermann et al. [1988] stated that this vocalization type in lesser galagos is associated with environmental and social disturbances, such as loud noises, unfamiliar objects or conspecifics, hostile interactions and potential predators. In accordance with this, we observed the highest occurrence of this vocalization type in the *G. senegalensis* group from Amersfoort, in which two adult males had recently been

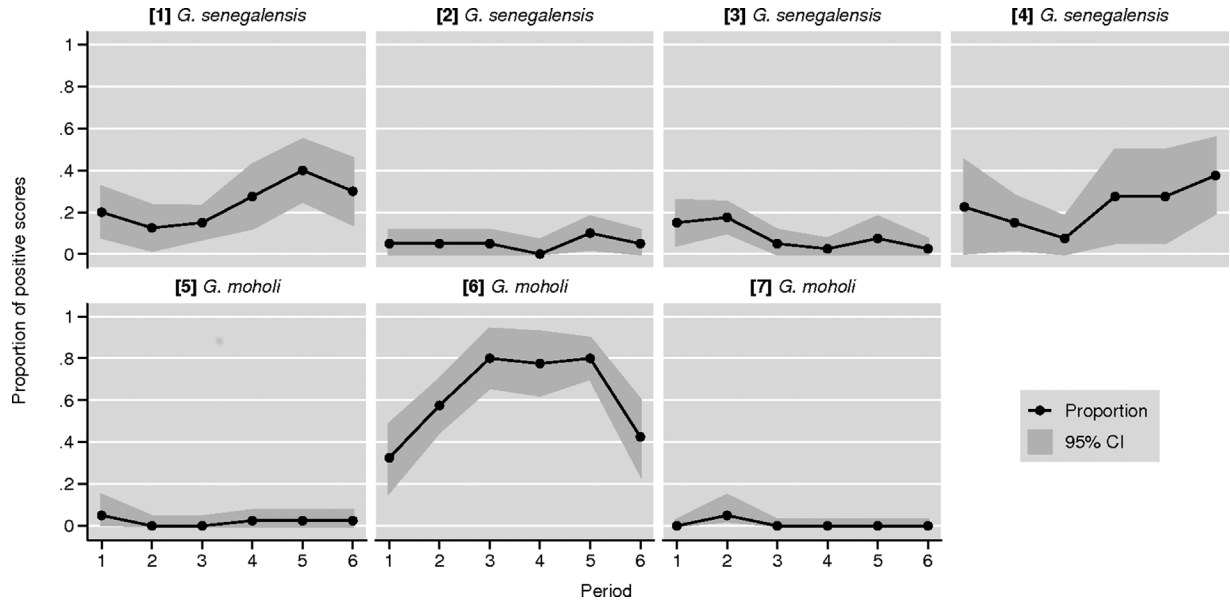

Fig. 5. Diel patterns of overall vocal activity (including all observed vocalization types) observed in all studied groups. Significant differences in diel vocal activity were found in the three most vocally active groups 1, 4, and 6. *Galago senegalensis* groups were the most vocally active at the beginning and at the end of their activity period, whereas one large *G. moholi* group showed an opposite pattern.

settled into one cage. The second highest contributor to this vocalization type was the *G. senegalensis* group from Prague, which included several individuals, notably, adult males that shared one exhibit. Both groups were also under the reversed day/night cycle and thus were exposed to disturbances from visitors and zoo staff. Moreover, the *G. senegalensis* group from Prague shared its exhibit with a pair of springhares, whose activity could also potentially lead to mild disturbances of galagos. The lowest production of this vocalization type was observed in the *G. moholi* groups that were housed off-exhibit without the reversed day/night cycle, were not exposed to disturbances from zoo staff and visitors, and did not share their space with other species of animals that could potentially disturb them.

The present study confirmed that the contact advertisement call that allows the most reliable species determination can be heard and successfully recorded from certain groups of lesser galagos living at zoos. Group companions have been reported previously to synchronize their activities via this vocalization type, and unfamiliar groups also usually

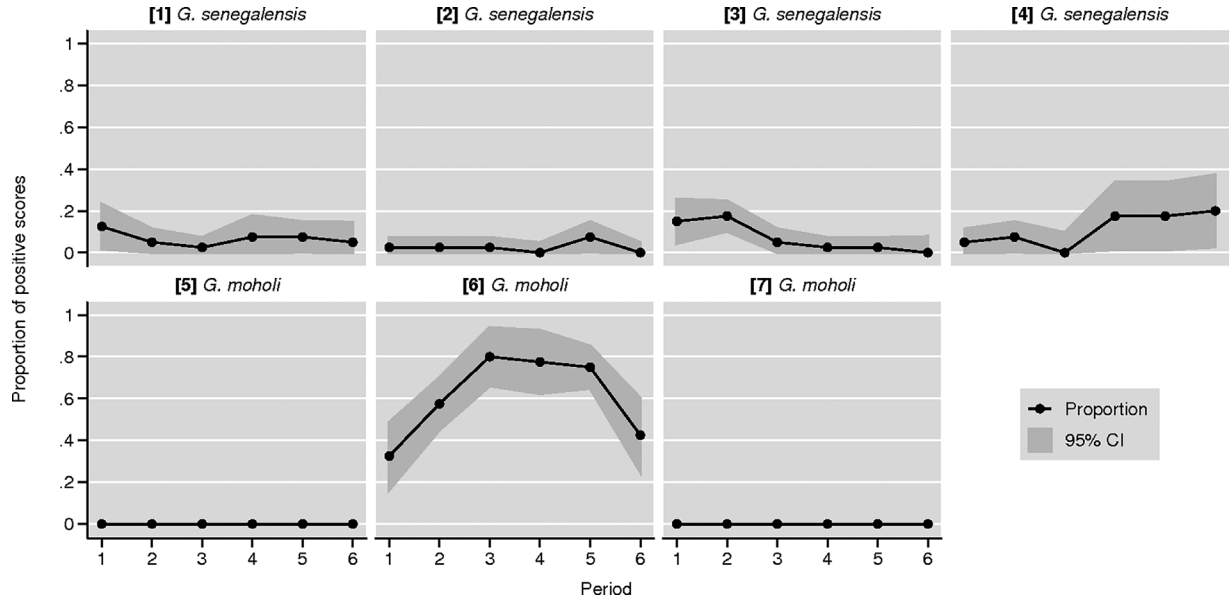

Fig. 6. Diel patterns of production of the "woo1/bark" advertisement call, which was the most diagnostic, was observed in all studied groups. Significant differences in diel production of this vocalization type were found in groups 3 and 4. Similarly to the overall vocal activity, the groups showed two distinct patterns of diel distribution of this vocalization.

answer each other's advertisement calls [Zimmermann, 1985; Zimmermann et al., 1988]. In accordance with this, we observed the highest contribution to this vocalization type from groups consisting of single individuals, couples, or small families housed in separate cages in a common off-exhibit room where they probably maintain contact via their advertisement calls. Additionally, unsurprisingly, we did not record this vocalization type from the two *G. moholi* groups comprising two members only and that had no acoustic and visual contact with other groups.

The "tjong/moan" attention/alarm vocalization was produced by the observed groups, although it was less common than the other two vocalization types. The group size and composition seemed to affect the occurrence of the "tjong/moan." The highest occurrence was observed in the *G. senegalensis* group from Prague, where five adult males shared one exhibit together with other group members. This is in accordance with previously published findings that this vocalization type is emitted during agonistic interactions, e.g., after fights between companions [Zimmermann, 1985; Schneiderová et al., 2014]. The rarest vocalization type was the "wik/chatter" agonistic vocalization. We failed to record it from most of the observed groups. We only recorded it from two *G. senegalensis* groups from Prague and Amersfoort, where disputes, especially between adult males, could be expected on the basis of the group composition.

We found a significantly unequal diel distribution of the overall vocal activity in the most vocally active groups. The patterns of diel distribution of the overall vocal activity to some extent corresponded to the patterns observed for the advertisement calls separately. Diel distribution of this call is of special interest in galagos because it has been suggested that distinct patterns of its diel distribution probably reflect the social behavior manifested by various species that can be otherwise hard to study in the field [Bearder et al., 2003]. Remarkably, we found different patterns of diel distribution of the advertisement call in the two studied species. *Galago senegalensis* groups were most vocally active at the beginning and at the end of their activity period. This is consistent with observations from the wild of lesser galagos producing advertisement calls especially at dawn and dusk [Bearder et al., 2003]. However, the large *G. moholi* group housed off-exhibit showed an opposite pattern; that is, this group was least vocally active at the beginning and at the end of their activity period. Based on our data, we can hardly conclude why this group showed such an unexpected pattern of vocal activity. Further studies based on empirical data and more captive groups or wild populations are needed to verify whether there are such behavioral differences between the two species or whether some factors were undetected by the present study that significantly affect vocal activity in the captive groups. Regarding our aim to find out the time when it is most effective to record species-specific vocalization types, the most promising time was the beginning or end of the activity period for the *G. senegalensis* groups. This was not entirely true in the case of the larger *G. moholi* group; however, it does not mean that recording at this time would fail. The high vocal activity of this group seemed to guarantee successful recording at any time of its activity period. Small *G. moholi* groups showed such low vocal activity that no conclusions can be made regarding the best time to record vocal activity for these groups.

The present study confirmed that loud species-specific vocalization types can be heard and recorded from lesser galagos living at zoos. Therefore, these vocalizations potentially could be further analyzed and used for species determination of these small primates in captivity. A comprehensive and reliable sound archive, which includes vocal profiles of the whole Galagidae family, exists and can be used for comparison of vocalization types recorded in captivity [Bearder et al., 2013]. This archive makes species determination based on bioacoustics highly efficient. Previously, the advertisement call has proven to be the most diagnostic for use in identifying the species [Zimmermann, 1985; Zimmermann et al., 1988]. However because the present study showed that production of this vocalization type could be limited in small captive groups, the "fwa/yap" attention/alarm vocalization could be used as an alternative at zoos. This vocalization type was recorded from each observed group in the present study, and it allows reliable discrimination between *G. senegalensis* and *G. moholi* [Zimmermann et al., 1988; Anderson et al., 2000]. Analysis that should verify species determination of lesser galagos at European zoos through the integration of bioacoustics and molecular/genetic data is currently ongoing [our unpublished data].

Qualitative evaluation of animal vocal behavior allows assessment of well-being in some animals [Ruiz-Miranda et al., 1998]. Quantitative evaluation of alarm vocalization types can be helpful when detecting higher stress levels in animals and can also be used as a measure of their welfare [Boinski et al., 1999]. The present study clearly demonstrates that both qualitative and quantitative differences exist in the vocal behavior of various groups of lesser galagos living at zoos. These groups differed in size and composition, and they were kept under different conditions. This might also be of interest and subject to further investigations into the successful keeping and breeding of these small primates at zoos. For example, the increased occurrence of some "fwa/yap" and "tjong/moan" attention/alarm vocalizations or the increased occurrence of "wik/chatter" agonistic vocalizations could indicate prolonged disputes between some animals. Early detection of such conflicts could allow keepers to reduce stress in some individuals or prevent injuries in others.

CONCLUSIONS

1. Loud vocalization types ("woo1/bark," "fwa/yap," "tjong/moan," and "wik/chatter") were spontaneously produced by lesser galagos living at zoos, and these vocalization types were more successfully recorded from larger and more diverse groups.

2. The most frequent vocalization type that was emitted by all the studied groups was the "fwa/yap" attention/alarm vocalization. Thus, the use of this vocalization is promising for the potential species determination of lesser galagos at zoos because it is also one of the species-specific vocalization types in their vocal repertoire. The rarest vocalization type was the agonistic "wik/chatter."
3. The most diagnostic vocalization type, the "woo1/bark" advertisement call, was most successfully recorded from larger groups, especially those in which single individuals, pairs or small family groups were housed separately in cages but had visual and acoustic contact with each other.
4. Distinct patterns of diel vocal activity were found in the study groups. Whereas the *G. senegalensis* groups were most vocally active at the beginning or end of their activity period, the *G. moholi* group showed an opposite pattern.
5. Both qualitative as well as quantitative differences exist in the vocal behavior of various lesser Galago groups in zoos. These differences could also be considered in the future for the evaluation of the well-being of these animals in captivity.

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