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ORIGINAL ARTICLE

Number of callers may affect the response to conspecific mobbing calls in great tits (*Parus major*)

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Abstract

Numerical competence—the ability to represent, discriminate, and process numerical quantity information—is a widespread cognitive ability in animals that influences survival and reproductive success. Little is known about the role of numerical competence during predator mobbing—when a prey moves toward and harasses a predator. Since being in a larger group dilutes the risk of injury or death during a mobbing event and large groups are more efficient than small groups at repelling predators, the capacity to evaluate the number of mobbers before joining the mobbing flock may be highly beneficial for individuals. We tested whether the strength of the mobbing response of great tits (*Parus major*), a songbird that frequently mobs predators, is related to the number of callers. The minimum distance to the loudspeaker tended to be lower, and the number of calls produced by great tits was higher during playbacks simulating several callers than during the playbacks of one caller. These results suggest that numerical competence plays a central role during mobbing and that great tits reduce uncertainty of information by collating information from several individuals. We suggest further studies testing whether birds use individual vocal discrimination to assess the number of heterospecifics during mobbing.

Significance statement

Can animals count? Although historically the ability to count has distinguished humans apart from the rest of the animal kingdom, studies in the last decades have shown that numerical competence, the ability to represent, discriminate, and process numerical quantity information, is a widespread cognitive ability in animals. While this competence influences an individual's survival success, little is known about the role of numerical competence during predator mobbing. Using a field-based playback experiment on a population of wild great tits (*Parus major*), we demonstrate that great tit responses to mobbing calls were affected by the number of individuals calling. The minimum distance to the loudspeaker tended to be lower and the number of calls produced by great tits tended to be higher during playbacks simulating multiple callers than during the playbacks of one caller. Thus, numerical assessments are used to decide whether or not to participate in mobbing responses.

Keywords Acoustic communication · Individual discrimination · Mobbing calls · Numerical competence · Paridae

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Introduction

When individuals share a common interest, such as driving a predator away, acting together is crucial to achieve the goal. In particular, during a mobbing event, individuals from the same and/or different species flock together to deter predators (Pettifor 1990; Krams and Krama 2002). In mobbing contexts, individuals use specific recruitment calls during these collective behaviors (Kalb et al. 2019). Predator-related recruitments calls (i.e., mobbing calls) are known to recruit both conspecifics and heterospecifics in collective mobbing behavior (Hurd 1996; Caro 2005; Randler and Förschler 2011;

Dutour et al. 2016). Yet, investing in mobbing (i.e., by approaching the predator and calling) entails individual risk (Sordahl 1990; Motta-Junior 2007), as injury is more likely. Individuals can show their investment in the mob by how closely they approach the threat, with a closer approach reflecting a higher urgency, and a greater investment (Randler and Vollmer 2013).

Like many other vocalizations, mobbing calls may convey information about the identity of the caller (Kennedy et al. 2009; Woods et al. 2018). Such distinctiveness may influence the decision to respond to these calls, as individuals could directly assess the number of birds calling. Indeed, the ability to evaluate the number of individuals from acoustic cues of a mobbing event could provide at least three distinct advantages. First, as the numbers of mobbers increase, the individual risk decreases (Hamilton 1971; Hogan et al. 2017; Wheatcroft and Price 2018). Second, given that large groups are more efficient than small groups at repelling predators (Dominey 1981; Robinson 1985; Krams et al. 2009), individuals in large groups could invest less energy and time in mobbing than individuals in small groups (Flasskamp 1994). And finally, a greater number of callers could indicate that the information about the predator is more reliable (Igic et al. 2019). Thus, the capacity to evaluate the number of mobbers before joining the mobbing flock may be highly beneficial for individuals when deciding to join.

Numerical competence (i.e., the ability to represent, discriminate, and process numerical quantity information, Nieder 2020) is a widespread cognitive ability in animals (from primates to insects; Brannon and Terrace 1998; Uller et al. 2003; Scarf et al. 2011; Potrich et al. 2015; Gazzola et al. 2018; Howard et al. 2018; Nieder 2019; Caicoya et al. 2020) that influences survival and reproductive success (e.g., in comparing food: Baker et al. 2011, or when guarding females, Carazo et al. 2012). Animals use numerical information in different ecological contexts, such as foraging, social interactions, and predator avoidance (Nieder 2020). Field studies have largely investigated the role of numerical competence in avoidance of predation by hiding (e.g., joining larger groups to increase the dilution effect: Hager and Helfman 1991; Mehlis et al. 2015; Nieder 2020), and few studies have focused on avoidance of predation by mobbing (Templeton and Greene 2007; Coomes et al. 2019; Nieder 2020). A recent experimental study in the jackdaw (*Corvus monedula*) provides the strongest case of numerical assessment during mobbing to date (Coomes et al. 2019). Indeed, Coomes et al. (2019) found that jackdaws recognize the number of callers when hearing mobbing calls and use this information to decide whether they join the mobbing event. Although costs and benefits when individuals confront a threat have been investigated, little is known about the role of numerical competence during mobbing events.

We tested whether the mobbing response of great tits (*Parus major*) is influenced by the number of callers. Great tits are small songbirds that produce mobbing calls to recruit conspecifics and heterospecifics to mob predators (Randler and Vollmer 2013; Dutour et al. 2016). Although great tits are known to respond to conspecific calls (Randler 2012; Dutour et al. 2017, 2020a) and are able to extract information from these calls (Kalb and Randler 2019), what remains unknown is whether great tits are able to discriminate the number of callers during mobbing, in a similar way to jackdaws (Coomes et al. 2019). Contrary to great tits which live and forage in pairs during breeding season and are not colonial, the jackdaw is a colonial breeding species, foraging in medium to large flocks. The level of sociality of these two species may influence their numerical competencies, but also the protocol in which these species are tested. Indeed, while Coomes et al. (2019) examined collective responses (number of recruits), we focused on individual-level responses in this study. We used playbacks simulating calling by one, three, or five individual callers to test whether great tits can assess the number of callers during a simulated acoustic response to a mobbing event (i.e., conspecifics giving mobbing calls). We focused on two behavioral variables directly linked to increased investment in mobbing because they make the bird more conspicuous therefore more noticeable by a potential predator: approaching to the loudspeaker, and calling (Dutour et al. 2017; Kalb et al. 2019). We expected great tits to come closer, and to call more, when there were five conspecifics calling, as opposed to when there was one.

Methods

Study site and species

Data were collected during playback experiments conducted on wild great tits inhabiting mixed deciduous-coniferous forests located in south-east France near Lyon (45.818992° N, 4.517753° E). As the focal birds were unbanded, we kept a minimum distance of at least 200 m between experimental sites to ensure independent measures of free-ranging great tits (Dutour et al. 2017; Kalb and Randler 2019). As the population density of great tits in our study area is quite high (15–30 breeding pairs per square-kilometer), we could space our experimental sites by 200 m, and still keep the probability of testing the same individual twice quite low (see Kalb and Randler 2019). Every experimental site was unique, and every playback track was unique and was played at only a single site. A total of 60 individuals were exposed to audio playback experiments (20 individuals per treatment condition; i.e., 1 caller, 3 callers, and 5 callers). All tests were conducted over a very short period during the breeding season (between 6

June and 16 June 2020) to avoid a seasonal effect (Dutour et al. 2019a).

Since the potential for great tits to respond to the number of callers depends on the calls of different individuals being acoustically distinct, we firstly conducted acoustic analyses showing that mobbing calls are individually distinctive (Supplementary Material 1, Fig. S1).

Call collection and stimuli preparation

We used great tit mobbing calls in response to predator mounts (tawny owl (*Strix aluco*) or sparrowhawk (*Accipiter nisus*), $N = 6$ recordings from 6 different individuals; 3 from each predator). These calls were obtained from our own recordings, and detailed information on call recordings has been provided elsewhere (Kalb et al. 2019). We also used mobbing calls obtained from the Xeno-Canto online database (http://www.xeno-canto.org/) with search criteria specifying the type of vocalization as "alarm call," quality "A" (i.e., highest recording quality, sampling rate 44.1 kHz; sample size 16 bits), and with no other bird species in the recording ($N = 14$ individuals) (Supplementary Material 2, Table S2). These calls have been used in previous studies (Dutour et al. 2019b; Salis et al. 2020).

We tested whether great tits responded more (i.e., coming closer to the speaker and producing more calls) to mobbing calls of several individuals than to one individual great tit giving mobbing calls. Playback tracks were designed to simulate calling by one (group size 1: GS1 treatment), three (GS3), or five (GS5) individuals (Coomes et al. 2019). Since the number of elements (i.e., the number of notes) in the alarm calls and the rate of delivery of elements within calls can communicate the degree of danger in birds (Leavesley and Magrath 2005; Templeton et al. 2005; Wheatcroft 2015; Dutour et al. 2020b), we kept the number of elements in the mobbing calls and the calling rate constant between playback tracks. In addition, the duty cycle (i.e., the amount of time a signal is present over a specified time) may be responsible for different responses to alarm callings (Landsborough et al. 2020); therefore, we kept the duty cycle constant (i.e., same amount of time per signal in all experimental conditions). All tracks were 30 s long and had the same structure, which comprised 15 calls (within the range of natural repetition rates during mobbing event, 26–34 calls/min; Carlson et al. 2019; Dutour et al. 2019b) and 10 elements per call (Carlson et al. 2019). Tracks comprising one individual caller had 15 different calls from one individual (GS1; Supplementary Material 3, Fig. S2a), and tracks comprising several callers had five different calls from three individual callers (GS3; Supplementary Material 3, Fig. S2b) or three different calls from five individual callers (GS5; Supplementary Material 3, Fig. S2c). Individual callers were randomly assigned to treatments to ensure that multiple-caller tracks had different combinations of individuals (Coomes et al. 2019; Supplementary Material 4 Table S3). In total, we constructed 20 unique soundtracks for each treatment (i.e., 60 soundtracks in total). To avoid pseudoreplication (Kroodsma et al. 2001), unique exemplars were used for each focal individual. Avisoft-SASLab software was used to create the playback tracks. Low-frequency noise (below 1 kHz) was filtered out, and the calls were amplified on a computer (Suzuki et al. 2016; Kalb and Randler 2019). All sound files were saved in WAV format.

Playback experiment

All playback experiments were conducted in a random order between 9:00 and 17:00 under calm and dry weather. Playbacks were performed when there were no other birds observed near the focal individual that might have interfered with the experiment. Nest positions were unknown. We controlled the pre-test behavior by only testing birds foraging, singing, or roosting alone. All tests in which another (previously undetected) bird displayed mobbing behavior before the focal bird were discarded ($N = 14$). Only one focal bird per playback experiment was tested to assure independence of the data. After finding a great tit, a remotely controlled speaker (Shopinnov 20W, frequency response 100 Hz–15 kHz) was hung from a tree at 1.5 m high from the ground (Suzuki et al. 2016) and 20 m away from the bird (Dutour et al. 2020a). Two observers with binoculars were positioned opposite each other at vantage points at least 10 m from the loudspeaker, a distance from which the focal individual's behavior was not disturbed (Suzuki et al. 2016; Dutour et al. 2020a), and observed the response to the playback. Although the observers were kept unaware of the selected soundtrack during all playback experiments to minimize observer bias, they could hear it, and thus were not blind to treatment. Each test was divided into a 30-s baseline of silence followed by playback of great tit calls for 30 s. To determine the tit's responses to the different treatments, we measured two behavioral responses: we counted the number of mobbing vocalizations during 30 s of playbacks (Carlson et al. 2017), and we measured the minimum distance to the speaker using a tape measure after the playback (i.e., we started to measure from the loudspeaker and followed a direct line to the closest place the bird approached; Kalb et al. 2019). A closer approach to the loudspeaker and a greater number of mobbing calls reflect a higher mobbing response from the focal bird, as both behaviors render it more conspicuous toward a potential predator.

Statistical analysis

Analyses were done in R 3.6.1. (R Development Core Team 2019). For our comparison of the difference in response of great tits to mobbing call playbacks, we ran linear model with treatment (GS1, GS3, and GS5) as a predictor term for the approach distance. Distance from speaker fits a Gaussian distribution. The significance of predictor term was tested using a non-sequential F test. We used a generalized linear model with a negative binomial distribution (*glm.nb*, package MASS) to analyze the number of calls since a preliminary analysis using the Poisson distribution for the error term indicated a substantial overdispersion in the dataset. Treatment was added as a predictor term. For both response variables, pairwise comparisons between treatments were performed (*glht*, package multcomp, Tukey comparison). As the results of the models indicated a marginal effect for the chosen significance threshold (5%), we calculated the effect size to infer the statistical difference of the contrast between one caller (GS1) and multiple callers (GS3 or GS5), treatment using Cohen's d for the approach distance and Cliff's d for the calling behavior. Finally, to test whether the presence/absence of specific individual callers in the playback had a biasing effect on the responses of great tits, we re-ran our models using the package MCMCglmm, including a multi-membership random term for each individual caller (Supplementary Material 5).

Results

A trend for decreased minimum distance with increased number of callers was detected, although not statistically significant ($N = 60$, LM: $F = 2.67$, df = 2, $P = 0.07$: Fig. 1a). The minimum distance tended to decrease as the number of callers in the playback track increased, but the difference only approached statistical significance between GS1 and GS5, and we detected no difference between GS1 versus GS3 or GS3 and GS5 (Table 1; Fig. 1a). Even if the model indicated a marginal effect for the chosen significance threshold, the effect size was medium when comparing GS1 and GS5 (Cohen's d = 0.73; 95% CI: 0.07; 1.4), reflecting a biological difference. The effect size was small when comparing GS1 and GS3 (Cohen's d = 0.29; 95% CI: − 0.35; 0.93).

Table 1 Pairwise comparisons between groups for both response variables: the minimum distance and the number of calls produced during 30 s by great tits. For all models, multiple comparisons were performed using a Tukey adjusted post hoc test. Marginally significant differences are indicated in italics

Comparisons	*t/z*	*P*
Minimum distance:		
GS3-GS1	− 0.98	0.59
GS5-GS1	− 2.30	*0.06*
GS5-GS3	− 1.32	0.39
Number of calls:		
GS3-GS1	2.28	*0.06*
GS5-GS1	1.28	0.41
GS5-GS3	− 1.01	0.57

Great tits tended to produce more calls when the number of callers increased, although this trend was also statistically non-significant in our model (N = 60, GLM: $\chi^2 = 5.18$, df = 2, $P = 0.07$: Fig. 1b). We found that great tits tended to produce more mobbing calls during the playback simulating three callers than during the playbacks of one caller (Table 1; Fig. 1b; a confidence interval (CI) excluding zero indicates a statistically significant result: Cliff's delta estimate: − 0.44; 95% CI: − 0.69; − 0.09). We found no differences between GS1 and GS5 (Cliff's delta estimate: − 0.27; 95% CI: − 0.58; 0.10) and between GS3 and GS5 (Table 1; Fig. 1b). Finally, the MCMCglmm analyses showed that the calls of no single individual were more influential than others (Supplementary Material 5, Table S4, Fig. S3).

Discussion

Little is known about the role of numerical competence during mobbing events in songbirds. Our study is the first that tested this assumption in parids and revealed that the number of calls and the minimum distance to the speaker were affected by the number of individuals calling, although this effect sometimes only approached statistical significance. This result parallels the findings of Coomes et al. (2019) who found that playbacks simulating several callers recruit more individuals than playbacks of one caller in jackdaws. Together, these results suggest that numerical competence could play a role in responses to conspecific mobbing calls and that great tits probably reduce uncertainty of information by collating information from several individuals (Wolf et al. 2013; Igic et al. 2019).

Concerning the minimum distance, the pattern followed the expectations with a closer approach (measured as minimum distance) during the playbacks simulating five callers followed by playbacks simulating three callers and one caller. The difference between GS1 and GS5 is the most extreme difference, facing only one caller versus five callers. The minimum distance approach is a well-documented behavioral response of great tits to predators and in a mobbing-related context (Randler 2012; Dutour et al. 2016, 2017; Kalb and Randler 2019), and a closer approach represents a higher investment in joining the mobbing flock (Randler and Vollmer 2013). Therefore, our study shows that great tits may respond more strongly when there are more individuals already mobbing. This suggests that great tits potentially have numerical competence and are able to discriminate acoustically between different conspecific individuals. Finally, great tits could feel safe to approach closer if there are sufficient numbers already mobbing. As the numbers of mobbers increases, the individual risk decreases (Wheatcroft and Price 2018). Following

Weber's law, the increase in response should be stronger between 1 and 3 callers than between 3 and 5.

Concerning the number of calls, great tits responded more strongly to the mobbing calls of three callers than one caller, so they responded as expected; however, we expected an even stronger response to playbacks of the mobbing calls of five callers but this was not the case. The number of calls produced by the focal bird was higher during playbacks simulating several callers (three and five callers) than during the playbacks of one caller (means respectively for one caller and multiple callers: 3.95 and 6.45). These results suggest that for great tits, it might only be important if a single individual is calling or several individuals. The detailed number of others calling might be less relevant. Only one other study has been conducted to date to assess the role of numerical competence during predator mobbing (Coomes et al. 2019). By measuring the number of recruits in total in wild jackdaws (a recruit was classified as any jackdaw that moved to within 20 m of the speaker and/or circled above the speaker), the authors found differences between GS1 and GS3, and GS1 and GS5, but not between GS3 and GS5 (Coomes et al. 2019). Two hypotheses, not mutually exclusive, could be suggested to explain why we did not find a difference between GS1 and GS5, while the study with jackdaws did. Firstly, the numerical competence of great tits may be lower than that of jackdaws, perhaps because the calls of individual great tits are less variable than those of jackdaws. Jackdaw calls could be more variable (Woods et al. 2018), and it would be easier for them to identify individuals contrary to great tits who could not distinguish as many different callers as jackdaws can. To look at the idea that individuals of different species have a different amount of variability in their calls, it could be interesting to compare calls variability in a larger number of species, and finally, collect data on mobbing numerical competence across these species. Secondly, these two species have differently levels of sociality. Jackdaws, in comparison with great tits, have a higher level of sociality and even breed in colonies (Henderson et al. 2000), so they may be able to distinguish between different individuals more easily than great tits. Great tits are often solitary breeding pairs during the breeding season (but flock together with con- and heterospecifics during the non-breeding season and are social during the winter seasons, Carlson et al. 2020) and are not colonial. Larger groups involve potentially larger number of interactions between individuals; hence, systems of communication should be more complex in order to have an efficient transfer of information. As great tits do not have this complexity when breeding, they aggregate in winter; thus, they may possess numerical competence. These results suggest that species with social systems, such as species living in fission-fusion societies, dominance hierarchies, or species living in groups with individual recognition, should have elaborated such recognition abilities. In accordance with this idea, previous playback experiments showed that species living in complex societies (e.g., lions *Panthera leo*, McComb et al. 1994; black howler monkeys, *Alouatta pigra*, Kitchen 2004; spotted hyaenas, *Crocuta crocuta*, Benson-Amram et al. 2011) discriminate between individuals based on their calls. The reason why great tits and jackdaws show numerical competency is probably because both species are social (although the level of sociality of great tits varies according to the seasons), but comparisons with non-social species would confirm this hypothesis. Finally, another explanation for why we found no difference in the number of calls made by the focal great tits during the

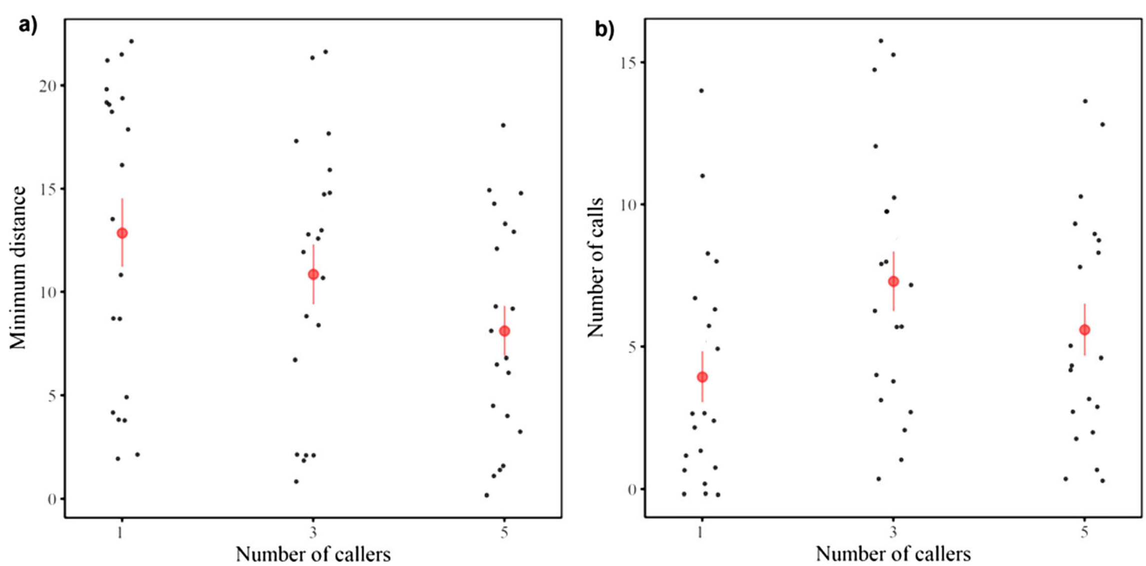

Fig. 1 Responses of great tits ($N = 60$ individuals). **a** Minimum distance (in meter) to the loudspeaker. **b** Number of calls produced during 30 s of playback. Each individual was exposed to only one treatment (GS1, GS3 and GS5), giving $N = 20$ per treatment. Black points are raw data from each playback trial; the mean and standard error for each number of callers are shown in red

playbacks simulating three and five callers may be that great tits stop increasing their calling rate when the number of individuals already calling reaches a certain number. Consequently, the production of calls may not increase linearly but rather reach a plateau. As our other variable (i.e., the minimum distance) depicts a difference in behavior toward the three treatments, it is therefore plausible that great tits do use numerical competence, but that the calling variable is not an adequate behavioral response to distinguish between the two higher treatments.

For great tits, such numerical competence could be important during winter, when they form flocks. Interestingly, such flocks are often constituted of several species (Dutour et al. 2019a; Carlson et al. 2020), and one could ask whether numerical competence could be used at the heterospecific level. Great tits are known to respond to other species' calls, such as blue tits (*Cyanistes caeruleus*) and chaffinches (*Fringilla coelebs*), during predator mobbing (Randler and Vollmer 2013; Dutour et al. 2016). Among the few studies investigating this aspect, the most recent showed that Australian magpies (*Gymnorhina tibicen*) responded similarly to alarm calls from two individuals of different species as they did to alarm calls from two individuals of the same species and responded more strongly to alarm calls coming from two callers versus one caller of a heterospecific species (Igic et al. 2019). Further studies should test whether birds use individual vocal discrimination to assess the number of heterospecifics during a mobbing event. In our case, for instance, it would be interesting to test if great tits use individual vocal discrimination to assess the number of chaffinches during a mobbing event. Another yet unstudied aspect is the between-species difference in mobbing responses (Randler and Vollmer 2013). Some species seem to be more reluctant in joining a mobbing flock compared with others, e.g., blue tits showed the highest commitment to join a mobbing flock, and chaffinches the lowest. This species-specific behavior might depend on the numerical competence of each species, suggesting that the more reluctant chaffinch may join a flock quicker when more other individuals are calling. So if some species can distinguish a higher number of individuals in a group, and some species cannot distinguish as many, this has consequences for how each species responds to the alarm calls.

Finally, in our experiments, all playbacks were played back from one speaker, suggesting to the receiver that all callers are sitting at the same spot. Future work should use different speakers at different locations to simulate callers in a more natural way. Perhaps, then, it would be more obvious to the receiver that there are different callers (in addition to the individual variation in the calls, it also would show different locations); thus, we would expect a stronger response.

In conclusion, our study indicates that the number of callers tended to influence the number of calls made by the focal individual, and the minimum distance that the great tit approached the speaker. These results suggest that great tits may use numerical competence to assess whether they respond to conspecific mobbing calls.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-021-02969-7.

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Data availability The datasets generated and analyzed during the current study and the R code are available as supplementary material.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All tested great tits returned to normal activity relatively quickly following playbacks, so we were confident that they were not unduly stressful. This study was conducted in accordance with the current laws in France and complied with the ethical rules set by University Lyon 1 concerning the use of wildlife species in research programs, but did not need any special permit.

Consent to participate and consent for publication Not applicable

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