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Conspecific density biases passive auditory surveys

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ABSTRACT. Surveys of vocalizing individuals are useful in detecting widely dispersed species that are hard to locate visually. We determined whether conspecific density affects spontaneous vocalizations of territorial Eagle Owls (*Bubo bubo*) and thus creates a bias in passive auditory surveys. We mainly listened to dusk call displays of 17 males breeding in two areas of high and low density from the beginning of call activity in October to the start of egg-laying in February. We detected differences in call behavior between males breeding in high density vs. low density. The nearest neighbor distance between breeding males strongly and positively affected call duration. Low density caused low detectability of male Eagle Owls, and later timing of the first call after sunset. Failing to incorporate conspecific density and nearest neighbor distances in surveys of territorial species may reduce the accuracy of population estimates.

SINOPSIS. **Sesgo en la densidad conspecifica de censos auditivos-pasivos**
Los censos de la vocalización de individuos son útiles para detectar especies que están ampliamente dispersadas y que son difíciles de localizar visualmente. Determinamos si la densidad conspecífica afectaba la vocalización espontánea de un buho (*Bubo bubo*) territorial y si ésta creaba sesgo en el censo auditivo-pasivo. Principalmente, nos dedicamos a escuchar durante el crepúsculo las llamadas de 17 machos reproductivos en dos áreas de alta y baja densidad. El trabajo se llevo a cabo desde octubre (cuando comienzan las llamadas) hasta febrero (cuando comienza la puesta de huevos). Detectamos diferencias en las llamadas entre machos en áreas de alta y baja densidad. La distancia entre machos reproductivos afectó marcada y positivamente la duración de las llamadas. Las áreas de baja densidad causaron baja detectabilidad de los buhos, y la hora a la cual se llevó a cabo la primera llamada luego de la puesta del sol. El fallar en incorporar la densidad de aves y la distancia entre los vecinos más cercanos en aves territoriales pudiera reducir la exactitud de estimados poblacionales cuando se utilicen censos de vocalización.

Key words: bias, *Bubo bubo*, call displays, density, Eagle Owl, passive auditory survey

Monitoring and estimating bird populations is common in bird studies (e.g., Ralph and Scott 1981; Verner 1985; Bibby et al. 1993). The extensive scientific literature on bird survey and census techniques mainly concerns the use and assessment of counting techniques for different purposes and the biases limiting their accuracy. Although many studies have addressed the sources of bias, this remains an area in need of further investigation (Verner 1985; Ralph et al. 1995).

Birds often reveal their presence vocally, and many species of birds are best detected from their vocal displays (Gibbons et al. 1996). Several factors affecting bird survey methods using spontaneous vocalizations have been identified, including among-observer variation, due to different censusing skills, motivation, or effort; the methodology, such as count duration, sample size, measurement units, and sampling strategies; habitat, because birds are easier to find in some habitats than in others; season and time of day, both causing variation in bird activity; weather, because extreme conditions affect both bird activity and the quality of observations; the size of the study area; and the species and its characteristics, such as detection distance, activity patterns, sex, age, social status, and density (e.g., Granholm 1983; Verner 1985; Bibby and Buckland 1987; Otter 1996; Schieck 1997; Poulin et al. 2000).

With respect to the possible effects of density on effectiveness and accuracy of sampling using birds' vocal displays, several authors demonstrated that sampling error increases with population size in high-density situations and that the observer misses a higher proportion of birds when conspecific density is high (Bart and Schoultz 1984). Few studies have investigated

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calling behavior in low-density situations. Birds seem to call less frequently in low-density areas (LaPerrière and Haugen 1972; Sutherland 1996; McShea and Rappole 1997; Legare et al. 1999), although small sample sizes in these studies make it difficult to draw conclusion and possible biases in counting methods were not quantified.

Surveys of vocalizing individuals are often used to detect species that are hard to detect visually. The Eagle Owl (*Bubo bubo*) is a territorial species widely distributed in Palearctic regions. It breeds in a variety of situations, mainly depending on abundance and distribution of prey, and is often surveyed by listening to spontaneous vocalizations (passive auditory surveys, hereafter PAS; Penteriani et al. 2000). In this species, Penteriani and Pinchera (1991) demonstrated that PAS generally provided better results than surveys based on broadcast surveys or vocal imitation of conspecific calls. Territorial defense is performed mostly by males, which are more vocal than females (Penteriani 1996).

We hypothesize that because call displays are costly (Kroodsma and Miller 1996), males without neighbors, or males with only distant neighbors, may invest less energy in calling activities than those in high-density populations. Males in low-density situations, characterized by large nearest neighbor distances between breeding sites, may derive no advantage from paying the socially imposed costs of signaling.

Our study examines whether conspecific density is related to the frequency and duration of spontaneous vocalizations in the Eagle Owl and thus represents a potential bias in PAS.

METHODS

Study area and data collection. We conducted PAS from October 1997 to July 2000 in the Luberon massif (southern France, 43°53′N, 5°24′E). Elevation ranged from 160 m in the Durance river valley to 1125 m on Grand Luberon ridge. The study area was characterized by a mosaic of cliffs, shrub vegetation (*Quercus coccifera, Thymus vulgaris* and *Rosmarinus officinalis*), Mediterranean forest (*Quercus ilex, Q. pubescens,* and *Pinus halepensis*), croplands, pastures, and fallow fields.

We conducted a preliminary survey of the total breeding pairs in the massif using different survey methods (Penteriani et al. 2001). We identified two sub-populations within the study area. Sub-populations differed in density of breeding pairs due to differences in availability of cliffs along an elevational gradient (Penteriani et al. 2001, 2002). The high-density sub-population averaged 31.6 nest sites/100 km^2, with several nearest neighbor distance of less than 1 km. The low-density sub-population averaged 19.6 nest sites/100 km^2, and the distance between nearest sites frequently exceeded 3 km (Penteriani et al. 2001, 2002). The difference in density between the two sub-populations was significant (χ^2_1 = 138.6, P = 0.001).

We listened to 17 breeding males on a monthly basis from early October (beginning of call activity) to mid-February (when they generally start egg-laying; Penteriani et al., 2002). Each male was sampled once per month within the study period. Nine and eight males bred within low-and high-density areas, respectively. Our PAS started 1 h before sunset and ended 2 h after sunset, when the males had left their song-posts for the hunting territories and ceased their vocal displays. Dusk represents one of the two main peaks of the daily calling activity of Eagle Owls, the other being dawn (Penteriani, unpubl. data). During each listening session, we recorded the time of the first and last call (the deep and booming *oohu,* the main call type of adult males (Penteriani 1996), as well as of all the intermediate ones; the duration of each vocal event (a series of single calls, determined by a stopwatch, hereafter named call duration; we identified the end of a series of calls when the last call was heard >60 s before the next one, and a value of 1 s was arbitrarily ascribed to one isolated call; Penteriani 1999); number of calls in each series; and number of series in each sunset session.

The sample size of 17 Eagle Owls was increased by a larger sample (N = 27) of 13 Eagle Owls nesting in the high-density area and 14 nesting in the low-density one to evaluate the frequency of individual detection, estimated as the percentage of PAS at dusk during which a male Eagle Owl was heard in the surroundings of its nest site.

During the five months of the study, we performed a total of 64 and 108 PAS at dusk lasting three hours, as with the first data set, in high- and low-density situations, respectively,

Table 1. Absolute values and means of three call parameters during the entire pre-laying period (from early October to mid-February) for male Eagle Owls in high- vs. low-density areas.

		Call duration (s)		Number of vocal events in each series		Number of series in each sunset session	
	N	min-max	x̄ ± SD	min-max	x̄ ± SD	min-max	x̄ ± SD
High density	8	174.7–4472.0	1182.6 ± 1018.2	59.1–387.0	96.2 ± 96.2	3.5–8.0	3.7 ± 3.7
Low density	9	30.0–497.2	257.4 ± 180.7	5.0–48.2	33.2 ± 30.5	1.0–2.6	2.1 ± 2.2

trying to distribute them evenly within the months.

We did not conduct observations on windy, cloudy, or rainy days, and recorded vocalizations from the same locations and from the same distance (approx. 500 m from the nesting cliff).

Statistical analyses. For each Eagle Owl a single mean value for each calling parameter was used. This was based on 5 mo × 4 wk/mo × 3 h listening per week (approximately 60 h of listening per owl).

To test the hypothesis that density might affect call displays, biasing the effectiveness of PAS, we investigated (Mann-Whitney *U*-test; Sokal and Rohlf 1995) the possible impact of high- vs. low-density situations on vocal behavior by testing for possible differences in time of the first call at sunset, and frequency of individual detection.

Additionally, we used linear regression to examine possible relationships between call duration and nearest neighbor distance between occupied nests (NND), as a descriptor of conspecific density, and between male detection rate (calculated as the number of sunset listening sessions taken to detect a male Eagle Owl) and NND. Because we found mean call duration to be significantly related to mean number of vocal events in each series ($r_s = 0.97$, $P < 0.0001$, $N = 17$), and mean number of series in each sunset session ($r_s = 0.81$, $P < 0.0001$, $N = 17$), we only used the mean call duration as an estimate of vocal activity of individual males in the regressions.

When it was not possible to collect all the information required to carry out each of the different statistical procedures for the overall data set, we ran the analyses on sub-samples. When necessary to avoid pseudoreplication, we used the mean of the variables for each individual male. All tests were two-tailed, and statistical significance was set at $P < 0.05$.

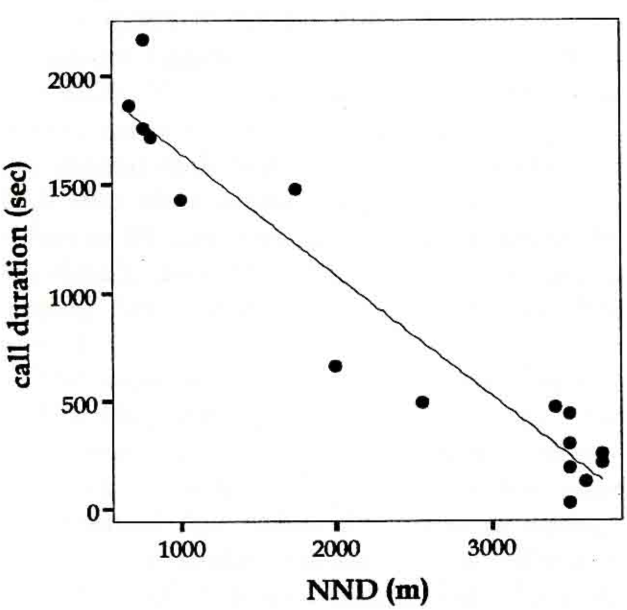

Fig. 1. Relationship between nearest neighbor distance (NND) and eagle owl call duration (s).

RESULTS

We detected differences in call behavior between males ($N = 8$) breeding in the high-density area and males ($N = 9$) in the low-density one (Table 1). The variability within sub-populations was mainly explained by male-male competition and individual quality (V. Penteriani, unpubl. data). These differences were significant in terms of mean call duration ($z = -3.368$, $P = 0.001$), mean number of vocal events ($z = -3.464$, $P = 0.001$) and series ($z = -2.953$, $P = 0.003$). Call duration was strongly positively correlated ($r^2 = 0.92$) with the NND (call duration = 2203.77 − 0.56 × NND; $t = -3.46$, $P = 0.004$): the lower the NND, the longer the call duration (Fig. 1).

Density significantly affected the detectability of male Eagle Owls near their nest sites ($z = -4.08$, $P = 0.0001$): the mean percentage of the species detection in high-density situa-

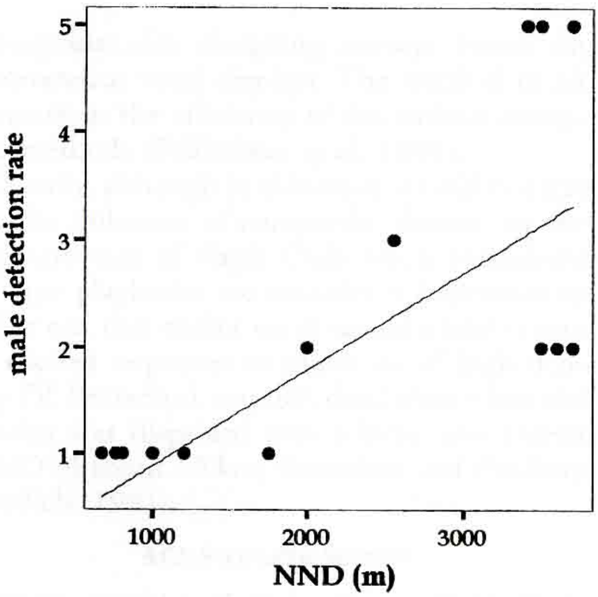

Fig. 2. Relationship between nearest neighbor distance (NND) and eagle owl detection rate, calculated as the number of sunset listening sessions taken to detect a male.

tions (95.7 ± 9.1%, minimum = 76.9%, maximum = 100%, $N = 13$) was more than double and less variable than that in low-density ones (47.8 ± 13.3%, minimum = 7.7%, maximum = 66.7%, $N = 14$). Moreover, starting with a NND of 2 km, the male detection rate increased in an unpredictable way, and the detected plateau level beyond which the male is always detected was represented by five sunset listening sessions (Fig. 2; male detection rate = 0.31 + 0.008 × NND; $r^2 = 0.47$).

Density significantly affected ($z = -1.828$, $P = 0.05$, $N = 85$) the time of the first call at sunset; males in high-density situations generally uttered their first dusk call earlier (11.2 ± 19.8 min after sunset, ranging from 14 min before to 68 min after sunset) than males in the low-density area (19.6 ± 19.1 min after sunset, ranging from 10 min before to 73 min after sunset).

The maximum distance at which we heard a male calling was estimated at 2 km, but the male *oohu* is generally audible within a detection radius not exceeding 1 km. In five cases we observed that, when the listening sessions took place in unsheltered areas and at a distance of 100 to 300 m from a calling male, the male immediately stopped calling when it detected the observer.

DISCUSSION

A high investment in vocal signaling in situations of low conspecific density, in which male-male competition is low, may be a waste of time and energy. Accommodation of territorial calling enables a male to minimize the cost of aggressive calling by setting its territoriality threshold to the locally prevailing conditions (Kroodsma and Miller 1996). Assessment is the foundation upon which communication systems are built, and individual behavior depends in part on evaluative reactions due to experience, which is a source of feedback sustaining or disrupting the activities that produce it (Owings and Morton 1998). When a species is not homogeneously distributed over an area (e.g., patches with high concentration of individuals vs. isolated ones), is strongly territorial, and is frequently engaged in communication networks, we should focus our attention on the possible impact of conspecific density on call displays. Due to the differential duration of the vocal activity of males in high- vs. low-density areas, PAS of territorial species that fail to incorporate conspecific density may reduce the accuracy of the resulting population estimates. We showed that the detection rate of Eagle Owls nesting in low-density situations was highly variable and lower than in high-density (Fig. 2). Under these circumstances, it is possible to underestimate the number of breeding Eagle Owls. The influence of density on call duration and timing in Eagle Owls may be so dramatic as to reduce the detection of a considerable portion of the breeding population. Two to five sunset listening sessions may be required to detect the species. Our results allow an observer to plan surveys with no *a priori* knowledge of potential density. Problems similar to those detected for the Eagle Owl may arise in surveys of other species that occupy a wide variety of nest sites and whose territoriality is maintained largely through call displays.

Estimating breeding density of bird species is an important part of population studies, and comparisons are widely used to assess the abundance of a species across years and in given areas or habitats. Biased estimates of breeding-pair density make it difficult to interpret existing data and prevent density comparisons between studies. Understanding factors that affect the natural calling activity of a species is thus a prerequisite for designing surveys based on spontaneous vocal displays. The result is in an increase in the efficiency of the various counting methods (Pollheimer et al. 1999).

Finally, although in this study we did not test for the influence of conspecific density on the response rate of Eagle Owls when stimulated by tape playbacks, we consider it important to point out that earlier we obtained a higher rate of elicited responses in situations of high density (V. Penteriani, unpubl. data) than when the species was dispersed over a large area (mean NND of about 10 km; Penteriani and Pinchera 1990a,b, 1991).

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