Abstract.—Vocalizations have the potential to allow the identification of individual birds. The practicalities of the technique were assessed for European Bitterns (Botaurus stellaris) and Black-throated Divers (Gavia arctica), two species that present different monitoring problems. The diurnal and seasonal pattern of booming behavior is predictable for bitterns; the less predictable pattern of Black-throated Diver vocalizations proved a significant limitation on the usefulness of the technique with this species. Spectrograms of the yodel vocalization of Black-throated Divers showed clear qualitative differences between individuals, whereas quantitative analysis of bittern booms was required to demonstrate individual distinctiveness. Within- and between-year identification of bitterns is complicated by a degree of variability in boom structure of some birds, but bitterns with relatively more stable booms were successfully re-identified. Black-throated Diver yodels showed striking between-year similarity. The factors that affect and limit the success of vocal individuality as an alternative to more conventional marking techniques are discussed.

INDIVIDUALIDAD VOCAL COMO HERRAMIENTA EN LOS CENSOS:
CONSIDERACIONES PRÁCTICAS ILUSTRADAS POR UN ESTUDIO DE DOS ESPECIES Raras

Sinopsis.—Las vocalizaciones tienen el potencial de permitir identificar aves individualmente. La practicalidad de la técnica se apreciaba en Botaurus stellaris y Gavia arctica, dos especies con diferentes problemas de monitoreo. El patrón diurno y estacionario de Botaurus es predecible; el patrón de las vocalizaciones de Gavia demostró que para esta especie la técnica tiene una utilidad muy limitada. Espectrogramas de la vocalización “tirolesa” de Gavia arctica mostraron claras diferencias cualitativas entre individuos, mientras que se necesitó un análisis cuantitativo de los “truenos” de Botaurus stellaris para demostrar individualidad distintiva. La identificación de Botaurus stellaris dentro de un mismo año y entre años se complicó por la variabilidad en la estructura de los “truenos” de algunas aves, pero individuos con “truenos” relativamente más estables se re-identificaron exitosamente. Las vocalizaciones “tirolesas” de Gavia arctica mostraron gran similaridad entre años. Se discuten los factores que afectan y limitan el éxito de usar la individualidad vocal como alternativa a otras técnicas más convencionales de marcar aves.

Considerable effort is often devoted to the conservation of rare or endangered bird species (e.g., Perrins et al. 1991). The effectiveness of these measures can only be judged by monitoring numbers and in some cases breeding performance and/or survival. Many species are straightforward
to monitor, but there are some whose habits and habitats make conventional monitoring virtually impossible. Common marking methods such as visible bands or radio-tags (Bibby et al. 1992) are limited by an ability to, and the desirability of, catching individuals.

Human observers can use qualitative and quantitative assessments of vocal characteristics to distinguish between individual birds. Qualitative methods include comparing sounds directly by ear, or visual comparisons of sound spectrograms. Quantitative methods include multivariate classification statistics such as discriminant function and cluster analyses. Computer-based cross-correlation and pattern recognition techniques are also becoming available (e.g., Williams and Slater 1991). Vocalizations that are individually distinctive to humans and that have subsequently been used for monitoring have been reported in a number of species, including American Woodcock (Philohela minor) (Beightol and Samuel 1973), Australian Kingfisher (Halcyon sancta) (Saunders and Woollet 1988), North American Common Loon (Gavia immer) (Miller and Dring 1988), Tawny Owl (Strix aluco) (Galeotti and Pavan 1991) and the European Bittern (Botaurus stellaris) (McGregor and Byle 1992, Turner 1924).

This paper reports on the practicalities of using individually distinctive vocalizations as a means to monitor numbers and annual survival for two species breeding in Britain, the European Bittern and the Black-throated Diver (Gavia arctica). These two species differ considerably in population size, vocalization complexity, habitats occupied and conservation problems. As such, they illustrate the costs, benefits and limitations of applying this technique to other species.

Bitterns live in dense Phragmites reedbeds and are rarely seen. The males have loud booming vocalizations, which are often the only indication of a bird's presence. There are now approximately 20 booming males in Britain, the population having declined partly due to the degradation of the specific reedbed habitat preferred by these birds (Day and Wilson 1978). Counting bitterns can be problematic because the low-frequency boom (~160 Hz) is difficult to locate and booming only occurs for part of the year. Identifying individual bitterns is important for accurate counts and mapping territories within a reedbed, information that is essential for decisions concerning habitat management. If individuals can be identified from one year to the next, site fidelity, survival and recruitment can be measured.

In the United Kingdom Black-throated Divers breed on large lochs in Northern Scotland, they are difficult to catch and are thought to be sensitive to human disturbance. The males produce a far-travelling yodel vocalization (Sjölander 1978). Visual counts of divers are fairly easy (cf., bitterns), but re-identification within- or between-years is impossible because of catching difficulties. The census issues of interest in the Black-throated Diver are the monitoring of site fidelity and survival in the long term, and ultimately whether the relatively low productivity of the British population (Campbell and Mudge 1990) should be a cause for concern.

Conventional banding techniques are unlikely to provide useful infor-
Vo...
A spectrogram (time in s, frequency in kHz) of a European Bittern boom train showing the terms used in description and analyses of the vocalization. This boom train has three booms. The first boom is usually preceded by a series of pumps (only one is shown in this figure) the other booms have two components, a first and main element. The six measurements used in the discriminant function analyses are the mean frequencies of: the main element of boom one (B1M1), the main element of boom two (B2M), and the first element of boom three (P3M); the interval between boom one and the first element of boom two (B1P2); and the duration of the first element of boom 3 (P3T) and its main element (B3T).

Black-throated Diver yodel vocalizations were counted and recorded in the Wester Ross area of Scotland from 0400–0900 and 1700–2200 hours (0900–1700 and 2200–0400 for at least one day out of seven). Therefore 24-h samples (over 2 d) were done before incubation (two in period 24 March–14 April, and three in period 23 April–25 May 1991) and after incubation (two in period 29 June–14 July 1992). Yodels were recorded from Divers found in the same territories in 1991–1992. There was no independent means of identifying the birds, but a Swedish study showed that Black-throated Divers invariably return to the same territory between years (Sjölander 1978). Playback of Black-throated Diver yodels and Red-throated Diver (Gavia stellata) flight calls to elicit vocalizations was done from the land, following the guidelines of Miller and Dring (1988) and under Scottish Natural Heritage (SNH) license.

Qualitative analysis of distinctiveness was based on naive observers judging which spectrograms of vocalizations most closely resembled spectrograms recorded in the same, or subsequent year. Background noise was erased from spectrograms to remove cues associated with recording conditions. The ability of observers was standardized to an extent by including two identical spectrograms in each comparison; if the observer failed
Vocal Individuality as a Census Tool

FIGURE 2. A spectrogram (time in s, frequency in kHz) of a Black-throated Diver yodel to show the terms used in description of the vocalization. Element 1 is commonly missing from phrase 1.

RESULTS

Recording vocalizations.—The pattern of seasonal variation in bittern booming differed between sites; at the North-West England site booming occurred from January to July, with high booming rates between late March and late June, whereas at South-East England sites booming occurred from March to June, with high rates from late March to late May. Regardless of season and site, most bittern booms occurred before dawn and after dusk (Fig. 3) and the rate of booming was highest at dawn and dusk (Fig. 4) with a significantly higher rate at dawn than at dusk (mean boom trains/min ± SE at dawn = 0.88 ± 0.20, at dusk = 0.52 ± 0.07; z = 2.51, P < 0.05, n = 21, non-parametric one-way analysis of variance).

Black-throated Divers were generally thought to yodel most commonly
during incubation (May), but we found that yodels were most common when adults first arrived at the breeding site (end of March–April) and when adults had chicks. Yodels were infrequent in May; yodelling occurred on 27 out of a total of 71 days, with a maximum of four yodelling bouts (of 1–5 yodels) heard in a day (10-h sampling period). This pattern was confirmed by an observer in 1992 (D. Jackson, pers. comm.). There was no obvious daily pattern of yodelling; before incubation, yodelling occurred around dawn and dusk (1991, n = three 24-h periods) and adults with chicks yodelled at dawn, dusk, mid-morning, mid-afternoon and midnight (1992, n = two 24-h periods). Attempts to elicit yodels with playback were relatively unsuccessful (cf., Miller and Dring 1988); six playbacks of Black-throated Diver yodels elicited no response in 1991, in 1992 yodels were elicited in three out of 19 playbacks, and playback of Red-throated Diver flight calls elicited yodels in two out of six playbacks. Black-throated Divers most commonly yodelled when an intruding diver was chased from the resident’s territory (yodels in 86% of such contexts, GG, pers. obs.), a situation that playback mimics poorly.

Vocal individuality.—Experience plays a major role in ability to identify bitterns by ear. In 1990–1991 two of the authors (GG, GT) with extensive knowledge of all English bitterns in the field could identify them all by a combination of differences in the booms and mapping territories. Also there was a significant correlation between the experience (= weeks listening to bitterns) of five volunteer RSPB wardens and correct matches of tape-recorded booms to actual booms (for three bitterns at one site, r = 0.95, n = 5, P < 0.05). The number of bitterns adversely affects ability to identify individuals by booms. A recent experiment showed that observers’ abilities to distinguish between recordings of booms decreases as the number of bitterns increases (GG and R. Sear, unpubl. data).

Spectrograms of recordings aid identification because they allow more extended comparisons than is possible for transitory vocalizations heard in the field or on recordings. They also provide a permanent archive for future comparisons. Twenty naive observers were given two spectrograms from each of 12 different bitterns present in 1990; they correctly matched 7.2 ± 1.9 (mean ± SE, n = 20) booms out of the 12 possible, considerably more than would be expected by chance.

Quantitative analysis of individual distinctiveness was based on step-wise discriminant function analysis of the 18 original variables taken from screen displays of spectrograms of thirteen bitterns from 1990. The six variables that this analysis determined contributed most to boom distinctiveness were: the mean (= max. – min. frequency/2) frequency of the first element of boom three (P3M), the mean frequency of the main

---

**Figure 3.** Counts of the number of boom trains given by one European Bittern (in territory NW2) during each hour of a 24-h period on three different dates in 1991. The time of dawn and dusk for each date is indicated.
FIGURE 4. Bittern boom rate (mean boom trains per min ± SE, n = 9 d) in relation to dawn and dusk (period 10) for NW1 in March 1991. Time is shown as 15-min periods centered on dawn and dusk.

Element of boom two (B2M), the duration of the first element of boom three (P3T), the inter-boom interval between boom one and boom two (B1P2), the duration of the main element of boom three (B3T) and the mean frequency of the main element of boom one (B1L1) (Fig. 1). Discriminant function analysis (DFA) of these six variables achieved 98.8% correct classification of individuals, with only one boom wrongly classified. Discriminant functions one and two explained 59.2% and 35.8% of the among-group variance, respectively. The usefulness of this subset of original variables was shown by a discriminant function jackknife analysis on a subset of booms of the same bitterns (data that were not used to create
the discriminant function equations). This jackknife analysis achieved 95.3% correct classification. These analyses confirm earlier studies showing that bittern booms are individually distinctive (McGregor and Byle 1992).

Spectrograms of Black-throated Diver yodels were correctly assigned to individuals by 15 naive observers (two spectrograms from each of six different divers), confirming our initial impressions that there are obvious qualitative cues to individual identity.

Within-year call stability.—Casual observations suggested that bittern booms changed during the season, most noticeably at the beginning of the season, and these have been referred to as “tuning-up” (Turner 1918) and “practice-calling” (Gentz 1965). Such booms are termed “poor” booms henceforth because they sound faint and unstructured, they are easily distinguishable from normal booms. Poor booms probably reflect development of the sound production apparatus as shown by Chapin (1922) and Gentz (1965) for the American Bittern, *Botaurus lentiginosus*. The proportion of poor booms was used as a measure of the within-year constancy of the vocalization. This differed between the two sites; for example, NW2 only produced poor booms up to early March whereas SE3 had high levels of poor booms throughout the season (Fig. 5). A second measure of boom constancy, the mean frequency of the main element of boom two (B2M, Fig. 1) confirmed this pattern (Fig. 5). NW2 and SE3 were representative of the two sites, as a consequence most bitterns in North-West England could be re-identified (by ear and using spectrograms) whereas most in the South-East could not.

The within-year stability of Black-throated Diver yodels could not be systematically investigated because of the limited range of recordings. Spectrograms of yodels from the same individual recorded 7 d apart (the longest available within-year interval) were similar, however.

Between-year stability.—Eight booming bitterns were recorded at the same sites in 1990 and 1991 (NW1–2; SE3, 5–7, 9–10 12–13). Eleven naive observers most commonly matched spectrograms of booms from territories NW1, NW2 and SE5 (5/11, 6/11 and 4/11, respectively). A quantitative comparison using DFA identified over 60% of booms recorded in 1990 from bitterns in territories NW1, NW2 and SE5 with recordings made at the same places in 1991, but less than 5% of recordings from seven other territories were identified in the same analysis. Interestingly, NW1, NW2 and SE5 also had the smallest within-year variation in booms. Independent confirmation that between-year boom similarity indicates the same individual bittern is provided by NW2, visually marked by a radio-tag in 1990 and 1991.

Four Black-throated Divers were recorded in the same location in 1991 and 1992, spectrograms of the yodels are very similar (Fig. 6).

DISCUSSION

Our results show that the factors affecting the feasibility of using individually distinctive vocalizations as a census tool are likely to vary from
species to species. In European Bitterns, we found that the difference between sites in boom constancy was problematic, whereas in Black-throated Divers the problem was to record enough yodels.

The ease of routinely collecting high quality recordings of the species should not be underestimated, particularly as rare species usually occur at low density in a few widely separated sites. In some species vocalizations may best be predicted by seasonal and diurnal timing (e.g., bittern booms), whereas in others the behavioral context of calling is the most important predictor (e.g., Black-throated Diver yodels). Information on
seasonal patterns of calling from observers with little experience of the demands of recording can be misleading, as we found for Black-throated Divers.

An independent means of identification, such as marking or radio-tagging, can corroborate interpretations based on vocal information. Our single marked bittern (NW2) showed that booms can be consistent within- and between-years and supports the idea that much of the between-year variability in booms reflected within-year variability rather than low site-fidelity. Similarly, the fact that banded Black-throated Divers returned to the same territory each year in Sweden (Sjölander 1978) supports our inference of high site fidelity from similarity of yodels.

It has been argued that bird vocalizations are almost certain to differ
Flc;um 6. Spectrograms (time in s, frequency in kHz) of three Black-throated Diver yodels recorded from the same sites in 1991 and 1992. Note the striking similarity for each diver between-years and the differences between divers within-years.

from individual to individual because of the vagaries of behavioral development and maturation even in species which do not learn their song (e.g., McGregor 1991b). Whether this level of variation is adequate for individual identification by humans can be assessed qualitatively or quantitatively. Both types of assessments are likely to be affected by the population size of the study species. Bitterns at the same site could be distin-
guished by ear by an experienced observer, but the maximum number of bitterns at any one site in Britain in 1992 was four. The technique may be of limited usefulness with large populations such as that at Lake Täkern in Sweden, with 12 km² of reedbeds and 32 booming bitterns in 1991 (L. Gezelius, pers. comm.).

An unexpected result of this study was the difference in pattern of bittern booms between the two English sites; bitterns in the North-West boomed for more of the year and produced fewer poor booms than those in the South-East. Autotte (1988) noted the opposite pattern in the booming period for American Bittern booms. Interestingly, bitterns in South-East England once boomed from January to late June (Turner 1918). The possibility that booming patterns are linked to physiological differences, perhaps due to age and condition, has yet to be investigated.

The most compelling reason for using individually distinctive vocalizations as a census tool is that the technique causes minimal disturbance, it is therefore particularly appropriate for species that are sensitive to disturbance and which cannot be readily caught or observed, often species of considerable conservation interest.

ACKNOWLEDGMENTS

Considerable thanks are due to Ken Smith of the RSPB for overseeing and managing the whole project and for many helpful comments on the manuscript. We thank: Doug Ireland and Digger Jackson for help with recording; RSPB Wardens John Wilson, Geoff Welsh, Mike Blackburn and Norman Sills, and SNH Wardens Tim Clifford and Bill Taylor for all their help and accommodation; the people who volunteered to take part in the qualitative experiments; Ted Miller, Rachel Scudamore, José Pedro Tavares, Xanthe Whittaker, an anonymous referee and the Editor for valuable comments on earlier versions of the paper. This project was mainly funded by a SERC CASE-studentship with the Royal Society for the Protection of Birds. Analysis equipment was funded by NERC and the Royal Society.

LITERATURE CITED


Received 24 Feb. 1993; accepted 29 Jul. 1993.