Can individually characteristic calls be used to identify long-distance movements of Corncrakes Crex crex?

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ORIGINAL ARTICLE

Can individually characteristic calls be used to identify long-distance movements of Corncrakes *Crex crex*?

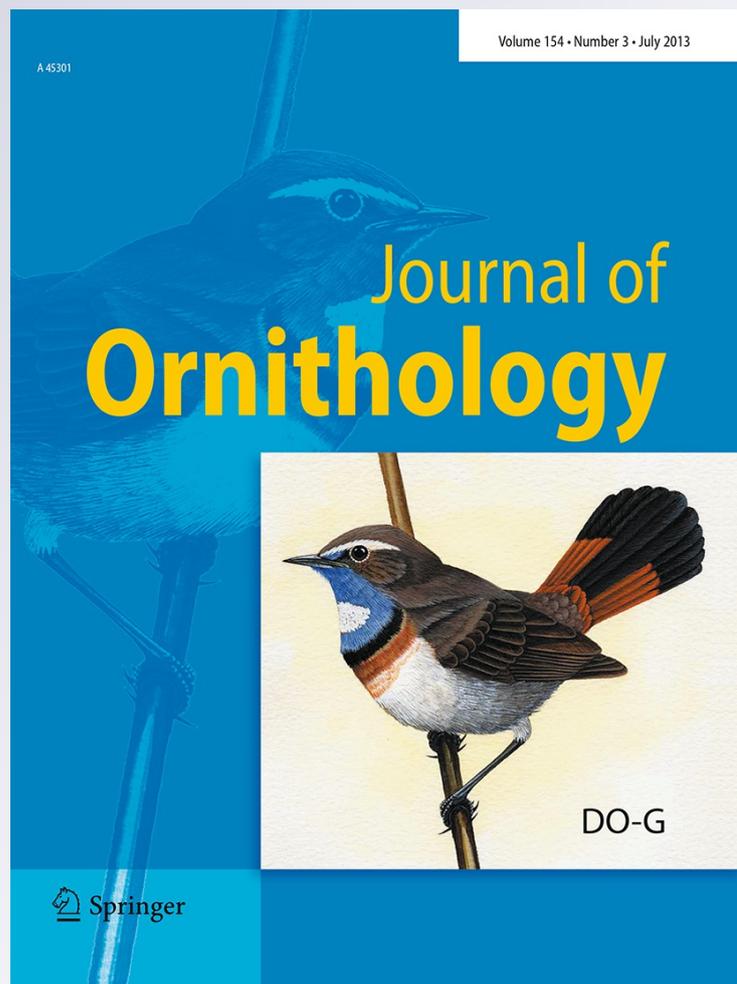**Gunvar Mikkelsen · Svein Dale · Thorstein Holtskog · Michał Budka · Tomasz S. Osiejuk**

Abstract Movements of animals at large spatial scales are important in ecology and conservation biology, but current methods for monitoring long-distance movements (e.g. ringing or telemetry) are resource demanding and limit sample sizes. Many birds have individually characteristic calls and songs, and recordings may provide an alternative method for monitoring movements. Previous studies have shown that Corncrake *Crex crex* night-time calls are individually characteristic. We recorded and analysed Corncrake calls from 60 different territories (30 % of all known territories) in two widely separated areas of Norway in one breeding season to assess the potential of recordings to identify individuals that had moved. Due to extensive mowing of meadows, many territories were used for only a short time, and Corncrakes appeared in new places throughout the breeding season, suggesting movements. By using recordings from the same territory during different nights as a measure of variability within individuals, and recordings from different territories during the same night as a measure of variability between individuals, discriminant analyses indicated that 86 pairwise comparisons of calls from different territories had a high probability (≥ 0.80) of being from the same bird.

Movements could be excluded for 20 of those pairs (23 %) because observations in the two territories overlapped in time. In another 26 cases (30 %), there was overlap in observation dates with other pairs that included the same recording. Thus, chance similarity between different individuals is a problem for individual recognition. Overlap in time decreased with increasing call similarity and, for pairs with very high call similarity (probability ≥ 0.95), only 5 % overlapped in time. Depending on degree of similarity in calls, the data suggested that 18–48 % of males made movements >10 km, and that the 60 recording sites only represented 31–45 different males. In conclusion, analyses of call recordings suggested that long-distance movements occurred, although positive identification of individual movements is difficult because the likelihood of chance similarity increases with the increasing number of birds recorded.

Keywords Dispersal · Population monitoring · Territory shifts · Vocal individuality

Zusammenfassung

Eignen sich individuelle Ruf-Charakteristika beim Wachtelkönig (*Crex crex*) dafür, Ortsveränderungen über weite Strecken zu verfolgen?

Bei Tieren spielen Ortsveränderungen über weitere Entfernungen in Ökologie und Naturschutz eine wichtige Rolle, aber die derzeitigen Methoden, solche Langstrecken-Bewegungen zu erfassen (wie z.B. Beringung oder Telemetrie) sind recht kostenintensiv und nur für kleine Stichproben möglich. Viele Vögel besitzen individuelle, charakteristische Rufe oder Gesänge, deren Aufnahmen eine alternative Methode bieten könnten, Langstrecken-Bewegungen zu erfassen und zu verfolgen. Frühere Untersuchungen haben

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gezeigt, daß die nächtlichen Rufe des Wachtelkönigs *Crex crex* für einzelne Individuen charakteristisch sind. Wir nahmen solche Rufe aus 60 verschiedenen Revieren (30 % aller dort bekannten Reviere) in zwei weitgehend voneinander getrennten Gegenden Norwegens während einer Brutzeit auf und untersuchten, ob diese Aufnahmen sich eignen würden, individuelle Vögel und deren Bewegungen zu identifizieren. Wegen des intensiven Mähens der Wiesen wurden viele Reviere nur für eine kurze Zeit benutzt, und während der ganzen Brutzeit tauchten die Wachtelkönige an allen möglichen unterschiedlichen Stellen auf, was starke Ortsveränderungen nahelegt. Wir benutzten Aufnahmen aus dem gleichen Revier, aber aus unterschiedlichen Nächten als Maß für die Variabilität bei Einzeltieren, sowie Aufnahmen aus unterschiedlichen Revieren, aber aus der gleichen Nacht als Maß für die Variabilität zwischen den Individuen. Eine Diskriminanzanalyse ergab, dass 86 Paarvergleiche von Rufen aus unterschiedlichen Revieren mit hoher Wahrscheinlichkeit (>0.80) von den gleichen Vögeln stammte. Für 20 dieser Paare (23 %) konnten Ortsveränderungen ausgeschlossen werden, weil die Beobachtungen in den beiden Revieren zeitlich überlappten. In weiteren 26 Fällen (30 %) gab es eine Überlappung von Beobachtungsdaten mit anderen Paaren in derselben Aufnahme. Daraus ist zu folgern, dass eine zufällige Ähnlichkeit zwischen unterschiedlichen Individuen am Problem der Einzeltier-Erkennung liegen kann. Die zeitliche Überlappung nahm mit wachsender Ähnlichkeit der Rufe ab, von den Paaren mit sehr großer Ruf-Ähnlichkeit (Wahrscheinlichkeit >0.95) überlappten nur 5 % zeitlich. Abhängig vom Grad der Ähnlichkeit legen diese Daten nahe, dass 18–48 % der Männchen Ortsveränderungen von mehr als 10 km machten und dass 60 Aufnahme-Areale nur 31–45 unterschiedliche Männchen repräsentierten. Die Analyse der Ton-Aufnahmen legt nahe, daß Ortsveränderungen über längere Distanzen vorkamen, wobei jedoch eine eindeutige Identifizierung der Bewegungen von Einzeltieren schwierig ist, weil die Wahrscheinlichkeit zufälliger Ähnlichkeit von Rufen mit wachsender Anzahl aufgenommener Tiere ansteigt.

Introduction

Understanding animal movements at large spatial scales is important for behavioural ecology, population ecology and conservation biology (e.g. Bullock et al. 2002; Clobert et al. 2001; Greenwood 1980; Hanski 1999). The empirical basis for understanding such movements is often limited because of methodological constraints (Koenig et al. 1996; MacDonald and Johnson 2001). Documenting movements of individually marked animals beyond small study areas can be extremely resource demanding so that sample sizes

remain small. General ringing schemes for birds rarely obtain recaptures of more than a few percent of all individuals ringed (Paradis et al. 1998). Specific telemetry studies may face challenges in capturing individuals to be tagged. Standard telemetry is often limited by transmitter range, and the likelihood of losing contact with a tagged individual increases the longer they move (Kenward et al. 2002). Satellite telemetry may overcome these problems, but high costs again limit sample sizes.

Many birds have individually characteristic songs and calls (Catchpole and Slater 2008), and birds themselves use this to discriminate between neighbours and strangers (e.g. Lovell and Lein 2005). However, this may also be used by researchers, and sound recordings may provide a fast, easy and cheap alternative way of recording individual identity, without the need to capture, handle and recapture individuals. Vocal individuality has been used to monitor populations (e.g. Darden et al. 2003; Hoodless et al. 2008; Tripp and Otter 2006), study individual turnover rates (Galeotti and Sacchi 2001) or record local movements (Rebbeck et al. 2001).

The endangered Corncrake *Crex crex* has individually characteristic night-time mating calls (see "Methods" for details), and Peake et al. (1998) reported that analyses of calls could identify up to 100 % of males correctly. This has previously been used to study movements on a local scale (within a 4-km^2 study area; Peake and McGregor 2001). Studies using ringing and telemetry have shown that Corncrakes can make long-distance movements of >10 km, sometimes even >100 km, during the breeding season (Schäffer and Koffijberg 2006), but it is unknown whether call characteristics can be used to identify long-distance movements in Corncrakes or any other species. Knowledge of the extent of movements is important for population estimation because movements may otherwise cause double-counting.

The Norwegian population of Corncrakes is well suited for testing whether recordings of calls can be used to identify long-distance movements. The population is small (29–231 males reported annually during 1995–2010) and has a limited distribution, mostly in one county in southwestern Norway and two counties in eastern Norway (Norwegian Directorate for Nature Management 2008). Furthermore, identification of the species can be reliable even for laymen due to the unique type of call, and public awareness of the problems facing this endangered species increases the chance that observations are reported to authorities. Finally, calling males often settle in hayfields which are mowed regularly (e.g. Holtskog 2010) so that many males are forced to move, suggesting that long-distance movements may occur.

In order to assess the usefulness of Corncrake calls for identifying potential long-distance movements, we recorded the calls of males from different sites in both main areas

for Corncrakes in Norway, separated by more than 300 km. The main issue is whether similarity in calls indicate that recordings are from the same individual, or if chance similarity between different individuals can prevent positive identification of movements. This was tested by comparing the proportion of cases in which similar recordings from different places overlapped in time, thereby excluding the possibility that they were from the same male.

Methods

Study species and study area

In Norway, Corncrakes occur mainly in hayfields, but in eastern areas also in grain fields (Holtskog 2010). Natural wet meadows are used more rarely. Corncrakes winter in tropical Africa, and return to breeding areas from the middle of May. Males call to attract females and to announce and defend territories. Females incubate and care for broods alone. When incubation starts, males may try to attract a new female (Schäffer and Koffijberg 2006). However, in Norway, most males are assumed to remain unpaired due to a lack of females (Norwegian Directorate for Nature Management 2008).

The study was conducted from May to July 2009 in eastern and south-western Norway, in the counties of Hedmark, Akershus, Oslo, Telemark, Vest-Agder and Rogaland. The main investigations of Corncrakes in eastern Norway were carried out in the northern part of Akershus (approximate location 60°10′N, 11°30′E) and in the southern part of Hedmark (approximate location 60°10′N, 12°00′E). Akershus and Hedmark are important agricultural areas, where grain production dominates, but smaller areas of pasture and hayfields also occur. The grain is usually harvested from the end of August to September. Other Corncrakes in eastern Norway were studied further south in Akershus, further north in Hedmark, and in Oslo and Telemark.

The main investigation of Corncrakes in south-western Norway was carried out in Jæren (approximate location 58°45′N, 5°35′E), a 1,070-km^2 lowland area at the coast of the southern part of Rogaland. Jæren is an important area for agricultural production, and consists mainly of pastures and hayfields; there are few grain fields here compared to eastern Norway. Hayfields are usually mowed 3–4 times from the end of May until September. Other Corncrakes in south-western Norway were studied in the northern part of Rogaland and in Vest-Agder.

General field methods

Agricultural areas suitable for Corncrakes were surveyed during the night-time calling period of males from 2300 hours until about 0400 hours. Call recordings (see below) were made whenever males in new sites were found. Due to an ongoing Action Plan for Corncrakes in Norway (Norwegian Directorate for Nature Management 2008), landowners reported Corncrakes to local authorities, and we were subsequently informed about these reports. In addition, birdwatchers reported Corncrakes on the website www.artsobservasjoner.no (Norwegian Biodiversity Information Centre) and www.nofoa.no (Norwegian Ornithological Society, Oslo and Akershus branch) which we checked continuously. We attempted to visit as many of the reported sites as possible to make call recordings. Furthermore, we visited previously recorded males as often as time permitted (often with one or a few days interval, in other cases >1 week between visits, median 2.5 days) to obtain information on length of territory use and whether hayfields used had been mowed. Information on territory use and mowing was supplemented by observations from birdwatchers, and overall information was available for 1–14 different dates for each territory (median = 4, n = 132). On several occasions, we made new call recordings of previously recorded males (see below). In general, we made short visits to as many different territories as possible each night, and areas to survey were chosen opportunistically to obtain recordings from new males.

Call recordings

Corncrake calls were recorded from a distance of 5–20 m for approximately 2–4 min with a Marantz PMD 620 digital recorder and a Sennheiser ME67 directional microphone. A total of 83 recordings from 60 different territories (30 % out of a total of 200 reported in 2009) were made in six different counties (number of recordings/number of territories): Rogaland (36/19), Vest-Agder (3/3), Telemark (2/2), Oslo (4/3), Akershus (24/21) and Hedmark (14/12). The criterion for considering Corncrakes to be in different territories was that individuals were calling more than 300 m from each other, or closer if calling at the same time ($n = 4$). Previous studies have shown that males rarely move more than 250 m between calling sites within one territory (Peake and McGregor 2001; Stowe and Hudson 1991).

Each Corncrake call consists of two syllables, hereafter referred to as syllables I and II, and two intervals (Fig. 1). Each syllable consists of a number of pulses of sound (usually 14–22) (Peake et al. 1998). Average length of pulses is 3–5 ms, and they are separated by intervals of 4–8 ms (Fig. 1). The time from the start of one pulse to the start of the next pulse has been defined as the pulse-to-pulse duration (PPD; Peake et al. 1998). Osiejuk et al. (2004) found that other song characters other than PPD, such as syllable lengths and interval lengths, varied within one breeding
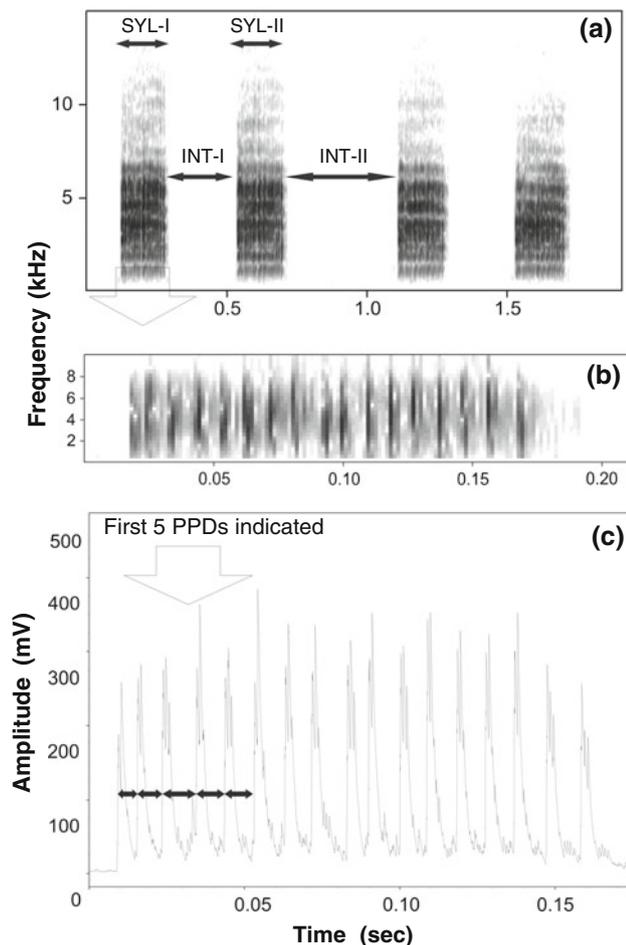
Fig. 1 Sonogram of male Corncrake *Crex crex* call showing **a** a typical sequence of calls with two syllables (*SYL-I* and *SYL-II*) and intervals (*INT-I* and *INT-II*), **b** detail of one syllable (*SYL-I*) with the structure of pulses visible, and **c** pulse-to-pulse durations (*PPD*) within one syllable; *black arrows* indicate the first five PPDs

season, and thus only PPD-values were used for individual call identification (cf. Peake et al. 1998). All recordings were made with 48.0 kHz/16 bit sampling rate. Because the recordings were also used in another study which also included recordings with a different sampling rate, we transformed all recordings to 22.05 kHz/16 bit sampling rate. Recordings were analysed using Avisoft-SASLab Pro version 4.39 software (Specht 2007). To remove low-frequency background noises, all recordings were high-pass filtered (0.5 kHz) with a FIR Time Domain Filter before PPD measurement. The first 10 calls without significant background noise were digitized from each bird for each recording session by using the following general settings of the sonogram window: FFT length = 512, frame % = 25, window = Hamming and temporal resolution = 98.43. These settings gave a measurement accuracy in time domain equal to 0.3628 ms. To measure PPD structure, we used the 'Pulse Train Analysis' function. Each syllable was measured separately. We used the 'rectification + exponential decay'

method for envelope detection. Initially, we started PPD measurements with the following settings: time constants = 1 ms, threshold =0.25 V, hysteresis = −12 dB, start/end threshold = −10 dB. Additionally, we always visually checked if all pulses were correctly detected. For recordings which were made at longer distances, we decreased threshold and hysteresis to detect all pulses.

Statistical analyses

The similarity in call characteristics between different recordings was analysed using linear discriminant function analyses (cf. Peake et al. 1998). Pairwise combinations of all the 83 different recordings were used, giving a total of 3,403 pairwise comparisons. Prior to analyses, pairs of recordings were classified into three groups. One group consisted of recordings from the same site during different nights and assumed to be from the same bird (termed 'same bird'). The second group consisted of recordings from different sites during the same night which should be from different birds (termed 'different bird'). All other pairs of recordings were termed 'other'. There was variation in the degree of our confidence that recordings from the same site represented the same bird. This was because there was a variable number of days between visits to the same sites so that territory turnover might have occurred, especially with increasing time between visits. The cases with lower confidence were classified as 'other' in one discriminant function analysis (hereafter referred to as the conservative classification), and 'same bird' in another discriminant function analysis (hereafter referred to as the liberal classification). The criteria for being 'same bird' in the conservative classification were set to gaps of maximum 1 week and maximum 250 m between recordings (distance according to Peake and McGregor 2001). The criteria for being 'same bird' in the liberal classification were set to gaps of up to 2 weeks and up to 600 m between recordings. Twenty pairs of recordings were classified as 'same bird' in the conservative classification (from 10 different sites; 8 sites recorded during two different nights and 2 sites during four different nights) and 29 pairs of recordings were classified as 'same bird' in the liberal classification (from 14 different sites; 9 sites recorded during two different nights, 3 sites during three different nights and 2 sites during four different nights).

Two syllable characters were used for individual call recognition: PPD in syllable I (hereafter referred to as PPD-I) and PPD in syllable II (PPD-II). The number of PPDs used in the linear discriminant function analyses was determined by the minimum number of pulses in each of the two syllables across recordings (cf. Peake et al. 1998). This resulted in analyses being based on means of 12 PPD-I

values or 14 PPD-II values for each recording. In total, six linear discriminant function analyses were carried out: (1) PPD-I values and conservative classification (CONS-I), (2) PPD-I values and liberal classification (LIB-I), (3) PPD-II values and conservative classification (CONS-II), (4) PPD-II values and liberal classification (LIB-II), (5) PPD-I and PPD-II values and conservative classification (CONS-I + II), and (6) PPD-I and PPD-II values and liberal classification (LIB-I + II). Based on results of the discriminant analyses, we present predicted (posterior) probabilities that pairs of recordings were from the same individual. Pairs of recordings originating from the same bird were expected to have high probabilities, whereas pairs of recordings from different birds should in general have low probabilities. The results of the discriminant analyses were cross-validated by using the leave-one-out method on the sample of pairs of recordings classified as 'same bird' (conservative classification, $n = 20$, liberal classification, $n = 29$) and 'different bird' ($n = 79$ in both classifications). A single pair was used as validation data and the remaining pairs as training data, and the process repeated for each pair to estimate the percentage of correct classifications.

For analyses of temporal overlap, we used average probabilities calculated from the probabilities of the four different discriminant function analyses (CONS-I, LIB-I, CONS-II and LIB-II). Only the pair of recordings with the highest probability was used when there were several pairs of recordings from the same sites. Minitab and SPSS 20 were used for statistical analyses.

Results

Territory use and mowing

Establishment of new territories occurred during a long period in May–July, and a total of 42 % of all new sites (56/132) were reported after 15 June (Fig. 2). Median duration of stay in one territory was 4 days (range = 1–28, $n = 82$ territories). The last observations in territories which were abandoned were close to mowing for 52 % of cases ($n = 80$; usually 1–3 days before mowing, in a few cases staying in edge habitat 1–2 days after mowing), suggesting that mowing caused abandonment. Territories were abandoned throughout June and July with 52 cases occurring before 15 June (i.e. 68 % of territories established before 15 June; Fig. 2). Thus, a large proportion of abandonments preceded many late territory establishments.

### Individual call identification

We made 83 call recordings from 60 different sites (11 sites recorded during two different nights, 3 sites during
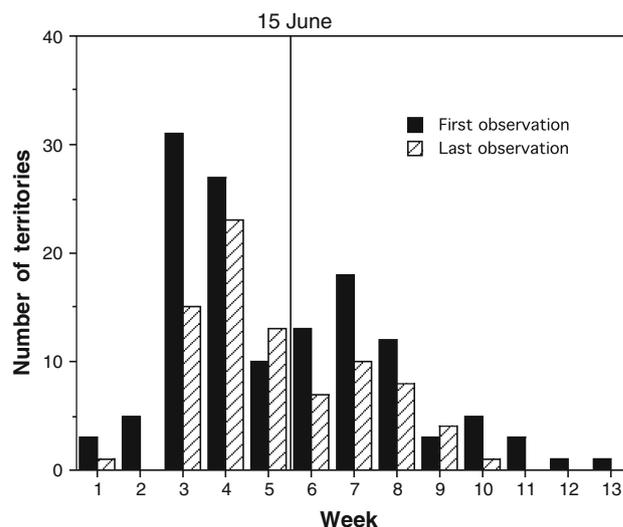

Fig. 2 Frequency distribution of time of first and last observations in territories of male Corncrakes in Norway. Sample size for first observations ($n = 132$) is larger than that for last observations ($n = 82$) because not all territories were monitored regularly until males disappeared. Week 1 started on 11 May and week 13 ended on 9 August

three different nights and 2 sites during four different nights). Discriminant analyses were used to calculate the probability that each of the pairwise combinations of the call recordings was from the same individual. The total distribution of all predicted probabilities ($n = 3,403$ pairwise combinations) based on, e.g., CONS-I was strongly left-skewed, but with a substantial number of cases with probabilities in the range 0.5–1.0 (Fig. 3). However, there was no clear separation between low and high probabilities (expected to correspond to pairs of recordings being from two different males or from the same male).

When restricting comparisons to cases which had been possible to define as 'different bird' or 'same bird' (see "Methods"), there was no overlap in predicted probabilities of 'different bird' (range = 0.00–0.78, $n = 79$) and 'same bird' (range = 0.83–0.99, $n = 20$) in the classification based on CONS-I (Fig. 4a). However, there was some overlap (16 %) in predicted probabilities of 'different bird' (range = 0.00–0.82, $n = 79$) and 'same bird' (range 0.32–0.99, $n = 29$) in the classification based on LIB-I (Fig. 4b), suggesting that the latter may contain 'same bird' cases which actually represented territory turnovers. Similarly, there was little overlap (2 %) in classifications based on CONS-II (19 of 20 'same birds' had probabilities ≥ 0.90), but more overlap (19 %) based on LIB-II (25 of 29 'same birds' had probabilities ≥ 0.85). Finally, there was no overlap in classifications based on CONS-I + II (all 'same birds' had probabilities ≥ 0.85), but more overlap (22 %) based on LIB-I + II (26 of 29 'same birds' had probabilities ≥ 0.85). Thus, these comparisons suggest that a limit
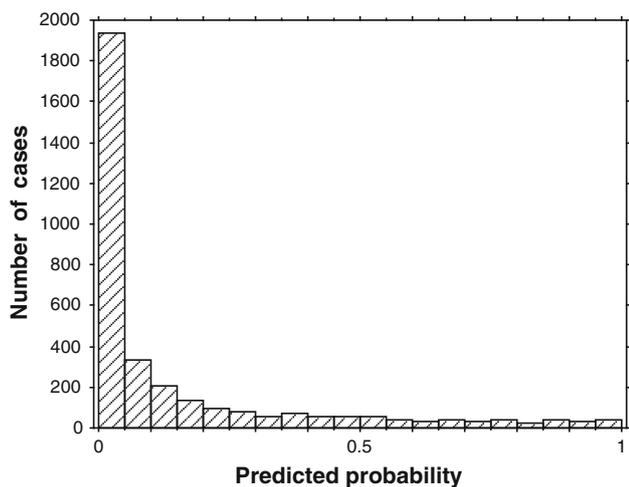
Fig. 3 Frequency distribution of predicted probabilities that pairs of Corncrake call recordings were from the same individual. Predicted probabilities for all possible pairwise combinations of 83 recordings ($n = 3,403$) were obtained from a conservative discriminant function analysis of mean pulse-to-pulse duration of syllable I (CONS-I)
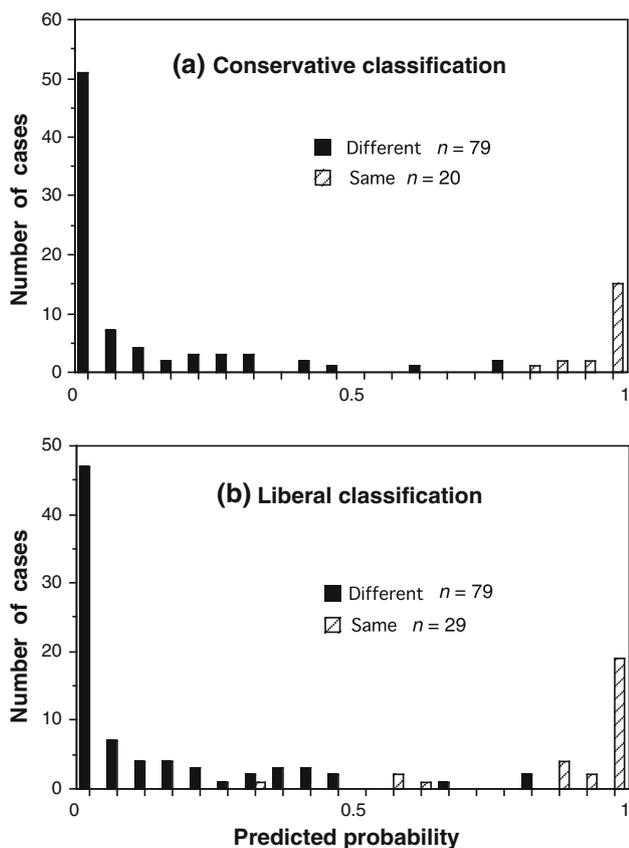
Fig. 4 Frequency distributions of predicted probabilities that pairs of Corncrake call recordings were from the same individual for cases where pairs were classified as 'same bird' (same territory during different nights) and 'different bird' (different territories during same night). Predicted probabilities were obtained from **a** a conservative discriminant function analysis (CONS-I) and **b** a liberal discriminant function analysis (LIB-I) of mean pulse-to-pulse duration of syllable I

using predicted probabilities ≥0.80 may separate most cases representing pairs of recordings being from the same male from cases representing different males, and that a conservative classification of 'same bird' appears to increase the separation.

Cross-validations indicated that percentage of correct classifications was 96.0 % for CONS-I, 94.9 % for CONS-II, 91.9 % for CONS-I + II, 90.7 % for LIB-I, 94.4 % for LIB-II, and 92.6 % for LIB-I + II (Wilks' lambda = 0.22–0.32, $P < 0.0001$ for all cross-validations). This also suggests that conservative classification of 'same bird' performed better than liberal classification. However, combining both PPDs does not lead to better classification. Thus, use of only PPD-I would suffice to separate same and different birds.

Temporal overlap

Among pairs of recordings termed 'other' (different territories in different nights), there was a total of 86 pairwise call comparisons which had average predicted probabilities (see "Methods") ≥0.80 and could potentially represent movements from one territory to another. Of these, there were 20 cases (23 %) in which presence in the two territories had overlapping dates which excludes the possibility that recordings were from the same male (except in unlikely cases of rapid turnover of territory owners). The proportion of such cases where similar calls likely represented different birds decreased as predicted probabilities increased (logistic regression of 86 pairs of recordings, $\chi^2 = 4.81$, $df = 1$, $P = 0.03$; Fig. 5). Among pairs with very high call similarity (probabilities ≥0.95), only 1/21 (5 %) of the cases had overlapping dates. In another 26 cases (30 %), two different pairs of recordings with high similarity included the same recording (i.e. recordings made in sites A and B, and sites A and C), and the other recordings (in sites B and C) in each pair overlapped in date so both implicated movements could not be correct at the same time.

Movements

Assuming that the remaining 40 pairs of recordings without conflicting temporal distribution each represented one and the same male, these represented 29 movements. Because of possible cases of multiple movements by the same individual (see below), 11 pairs of recordings dropped out because they would not represent an independent movement (i.e. for a male moving from A to B and then to C, the pairs AB and BC represented movements, but not AC). A total of eight individuals appeared to make more than one movement. Thus, a total of 19 individuals made the 29 presumed movements
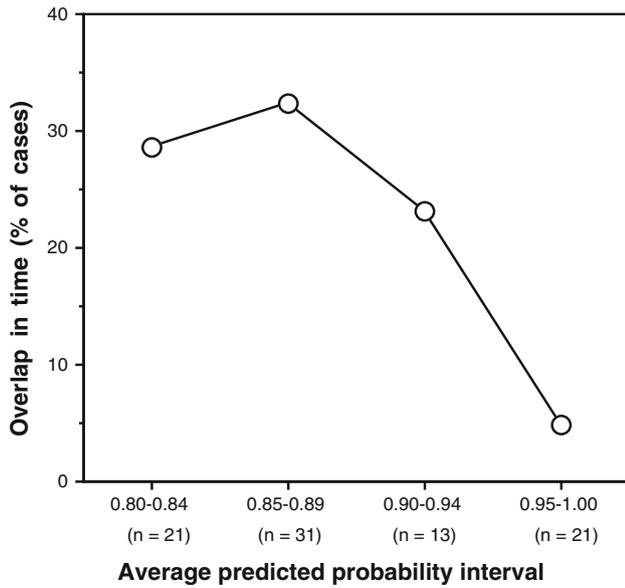
Fig. 5 Proportion of cases in which pairs of Corncrake call recordings had overlap in time (excluding the possibility that they were from the same male) in relation to average predicted probabilities obtained from four discriminant function analyses (CONS-I, LIB-I, CONS-II, LIB-II) of mean pulse-to-pulse duration of call syllables
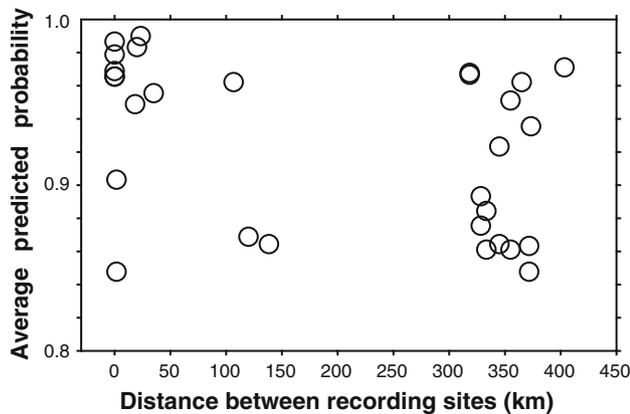
Fig. 6 Plot of average predicted probability that pairs of Corncrake call recordings were from the same male in relation to the distance between recording sites. Predicted probabilities were averaged from four discriminant function analyses (CONS-I, LIB-I, CONS-II, LIB-II) of mean pulse-to-pulse duration of call syllables. The sample ($n = 29$) includes only pairs without overlap in time and probability ≥ 0.80, and represent the most likely cases of movements of males from one territory to another

(median = 318 km, range =0.3–404 km; Fig. 6). Distances >300 km represented movements between SW and E Norway. There were also presumed long-distance movements among pairs of recordings with very high call similarity (probabilities ≥ 0.95; Fig. 6). Depending on the degree of similarity in calls, the data suggested that 18–48 % of males made movements >10 km, and 24–61 % made

movements ≥ 0.3 km (lower value includes only movements where probabilities ≥ 0.95, upper value where probabilities ≥ 0.80; proportions moving calculated from implicated numbers of 31 and 45 different males using the 60 sites with recordings).

Discussion

Call recordings and identification of individuals

To identify possible cases of movements, pairwise comparisons of all call recordings were made. The vast majority of pairs of recordings had low similarity in discriminant function analyses, suggesting that cases of high similarity may represent the same bird. By using similarities between recordings from the same territory during different nights (presumed to be the same bird), and between recordings from different territories during the same night (presumed to be different birds), we found that predicted probabilities ≥ 0.80 were likely to represent pairs of recordings from the same bird. The separation of 'same' and 'different' pairs was better using the conservative classification (shorter time and distance between two recordings assumed to be from the same bird) than the liberal classification (also including cases with somewhat longer time and distance; see "Methods"). Thus, the larger overlap between 'same' and 'different' bird in the liberal classification may be interpreted as an increased frequency of territory turnover which causes misclassification of 'same' birds. Our results suggested that separation of 'same' and 'different' birds was approximately similar for the two syllables in a Corncrake call, but that combining them in one analysis did not lead to better classification. The highest rate of correct classifications was achieved with CONS-I (96.0 %), and it should therefore be sufficient to analyse only PPD-I in order to separate same and different birds.

Separation of 'same' and 'different' birds seemed to be constrained by cases of chance similarity between different individuals. Even in the conservative classification, predicted probabilities for 'different' birds seemed to have a thin, but long tail to the right up to probability = 0.78 (Fig. 4a). The problem of chance similarity can be expected to increase with increasing population size (and increasing number of males recorded; Xia et al. 2012). This problem cannot be overcome with more sophisticated measurements simply because there is an upper limit to the number of unique pulse-to-pulse durations that can exist given the temporal structure of Corncrake calls. Thus, call recordings may not be suitable for 100 % positive identification of movements, but may just show that two recordings have a quite high probability of being from the same individual.

However, this may be sufficient for a variety of purposes such as estimating relative frequencies of movements and degree of double-counting of individuals when comparing different populations (see below). On the other hand, for studies of individual behaviour, individual identity based on calls will only work with a high degree of confidence in small populations where the likelihood of chance similarity between different individuals is low.

Another possible problem for using calls to identify individuals is variation between recordings from the same bird. Previous studies have indicated that pulse-to-pulse durations (PPD) vary little within individuals, whereas, e.g., interval length between syllables and syllable length depend on aggressive motivation, body size and time of season, and do not signal individual identity (Osiejuk et al. 2004; Ręk and Osiejuk 2010). However, in the conservative classification, presumed 'same' birds had predicted probabilities down to 0.83, and with a larger sample size values might be even lower. Thus, there is also some variation within individuals regarding PPD, but it is not known if this is due to random variation in call production or if such variation has a signal function.

The first source of error (chance similarity between different individuals) was illustrated in our study by cases in which pairs of recordings with high similarity could not be from the same individual because of temporal overlap in use of the two territories. Such cases had average predicted probabilities up to 0.96, although there was only one case ≥0.95 and most cases had predicted probability <0.90. This suggests that the value of call analysis depends on good field data on arrival and departure times for each territory, in order to exclude as many cases as possible of territory occupancies which cannot be by the same individual. This cannot, however, remove all cases of chance similarity, and we conclude that all cases of presumed movements have a certain probability of being correct, but it appears that, when the predicted probabilities from the discriminant analyses is ≥0.95, the risk of wrong classifications is very low. As mentioned above, there is an upper limit to how many individually characteristic PPD-values can exist and there is also some individual variation. Thus, there seems to be limited scope for using improved call characterisation to refine analyses.

It should also be noted that, if call similarity is used to reveal multiple singing sites for individuals in order to avoid double-counting (overestimation of population size), the problem of chance similarity between different individuals will introduce a concurrent underestimation because different individuals with similar calls would be counted as only one individual. We suggest that the latter error will be small relative to the number of movements revealed in populations where movements are common, and where there is thus a potential for overestimation.

However, if there are populations with little or no movements, using call similarity analysis might actually introduce an overall slight underestimation because the few cases of call similarity may be due mostly to chance similarity rather than indicating movements.

Evidence for movements

Previous studies of Corncrakes in Poland and Great Britain (Hoffmann 1997 cited in Schäffer 1999; Schäffer and Koffijberg 2006; Stowe and Hudson 1991) have shown that males may move within the breeding season, sometimes distances >100 km, due to disturbance or in search of females. Ringing of Corncrakes in Norway has documented one movement of 132 km within a breeding season (Mikkelsen 2010), and one of our birds was recaptured after a movement of 67 km within the breeding season. However, because most ringing of Corncrakes in Norway has taken place in a small area, most recaptures have shown shorter movements (median 14 km; Mikkelsen 2010).

The temporal pattern of first observations of Corncrakes in territories in Norway suggested that arrivals occurred during a very long period. A large proportion of first observations were after 15 June. Arrival of other migratory species in our study areas has ceased well before this date. Furthermore, last observations in territories were often long before late arrivals, and duration of stay in each territory was short, suggesting that birds leave from some territories and settle in new places during the breeding season. One obvious possible cause of departures is related to the species' habitat selection, preferring hayfields (Holtskog 2010). Hayfields in Norway are mowed two or more times in a summer, most frequently and earliest in the southwestern part of the country (Jæren). In this area, the season's first mowing started in the end of May and early June after about 17 male Corncrakes had arrived. Mowing was highly synchronous so that about a week later almost no hayfields were uncut, and hayfields did not reach suitable height for Corncrakes again before the end of June. Thus, during the period after first mowing, only 4 males were recorded. These observations strongly suggest that Corncrakes in Norway are likely to change territory quite often. Green et al. (1997) and Schäffer and Koffijberg (2006) also suggested that arrivals after 15 June were likely to involve males that had been in other sites earlier the same breeding season.

Movements implicated from call recordings

The results of the discriminant analyses and analyses of temporal overlap suggested that the majority of cases, in which pairs of recordings from different territories and

different nights had predicted probabilities >0.80, were likely to represent actual movements. A large proportion of the most likely cases of movements were >10 km, also the case when restricting the sample to those which had predicted probabilities ≥0.95. Many were even >300 km, which represented movements between the two study areas, i.e. between south-western Norway and eastern Norway. There were even recordings which suggested that some males moved from south-west to eastern early in the season, and then back again later in the season. Given that mowing almost completely eliminated suitable habitat in the south-western area early in the season, it is not surprising that they may have had to go far to find suitable habitat. Between the two study areas are mountains, forests and very little farmland, so despite the distance the two areas are more or less habitat neighbours.

Habitat loss and other forms of disturbance may force males to move to new places. However, not all cases of likely movements were caused by mowing. Sometimes, males disappeared well before mowing, or birds which disappeared used grain fields which were not harvested until after the breeding season. Lack of females may be another reason for movements of males within the breeding season (Dale et al. 2005). Small and isolated populations often lack females and therefore have a male-biased sex ratio (Dale 2001; Donald 2007). The Norwegian population of Corncrakes is relatively isolated from other populations in Europe and seems to have very few females (Norwegian Directorate for Nature Management 2008). Thus, some males may have abandoned territories because of a lack of females. Studies of other species with a male-biased sex ratio have shown that males abandoning a territory have a surprising ability to move quickly across the landscape and locate new breeding areas (Dale et al. 2006).

Conservation implications

Management of small and endangered populations often depends on accurate knowledge of population size and population trends. Our discriminant analyses suggested that a number of recordings from different places actually represented the same male. Thus, movements within Norway may cause double-counting of males. Previously, there has been focus on the issue of whether several observations in nearby areas represent one or several males, but there has been no strategy to handle the possibility that observations in different parts of Norway may represent the same birds (Norwegian Directorate for Nature Management 2008). Our results suggested that at least about a quarter of males moved, but possibly as much as 70 %, compared to 85 % in a previous study (Hoffmann 1997 cited in Schäffer 1999). The 60 recording sites may have

represented only 31–45 different individuals. Thus, the Norwegian Corncrake population could in the worst case be only half as large as previously assumed. In the Ortolan Bunting *Emberiza hortulana*, Dale (2009) found that frequent movements within the breeding season caused an overestimation of population size of 6–21 %, but only 6–17 % of males moved within 1 year, much less than our indications for Norwegian Corncrakes.

Given the possible problem of double-counting, managers need methods for estimating actual population size. Because capturing Corncrakes is time-consuming and difficult, ringing, telemetry or DNA-samples may not be realistic options for population estimation. Our analyses suggest that recording calls may give an indication of the scale of movements between sites. However, we have identified two important challenges with this method: call variation within individuals and chance similarity between different individuals. Detailed call analyses and monitoring of territory use may help, but will not make this method completely reliable. Thus, although Peake et al. (1998) reported that discriminant analyses had a high success rate in identifying individual males from calls even with a larger number of different birds ($n = 62$) than in our dataset, our analyses suggest that in general there will be a decreasing rate of correct identifications when number of birds involved increases, due to increasing number of cases of chance similarity (Xia et al. 2012). Furthermore, we note that discriminant analyses of our dataset also gave a large percentage of correct classifications (up to 96 %), but including information about territory use showed that such figures are misleading because many cases of pairs of recordings with high similarity had conflicting temporal distribution. This should also be considered in studies of other species using vocal individuality for population monitoring (cf. Darden et al. 2003; Hoodless et al. 2008; Tripp and Otter 2006).

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