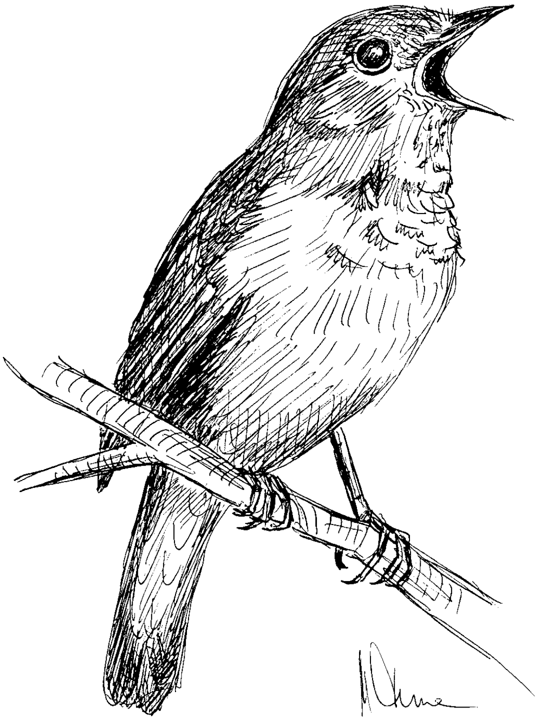
Singing activity and spatial behaviour as sexually selected traits in the Nightingale *Luscinia megarhynchos*



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Abstract

I examined singing activity and spatial behaviour of male nightingales with regard to possible functions in mate attraction, territory defence, and sperm competition.
Male nightingales sang at night before pair formation. They stopped nocturnal song upon pairing, but resumed it if their mate deserted. In contrast, unmated males sang nocturnal song throughout the breeding season. These findings suggest that nocturnal song plays a role in mate attraction.
Diurnal singing activity was highest in the hour before sunrise. This pattern was consistent throughout the breeding cycle and was hardly influenced by mating status, indicating that mate attraction is not the main function of the "dawn chorus" in the nightingale. I tested the alternative hypothesis that territorial males sing at dawn to defend their territory against non-territorial males: I translocated unpaired males to the study site (the „Petite Camargue Alsacienne“) and found that the radio-tagged males made extensive excursions visiting several singing males at dawn, but after dawn remained stationary outside occupied territories. These results suggest that non-territorial males use the dawn chorus to assess singing residents or territory occupancy. It also appears that dawn singing of territorial males is important to announce territory occupancy to non-territorial males and thus to defend the territory.
In contrast to the hour before sunrise, singing activity later in morning was strongly influenced by the reproductive state of females and peaked during the egg-laying period. This elevated singing activity may not serve primarily to repel cuckolder males pursuing extrapair copulations, since during the morning hours when egg-laying takes place, copulations are thought to less likely result in fertilization than in the days before egg-laying. Accordingly, male nightingales showed the greatest distances to their mates in the morning hours during the egg-laying period. Furthermore, extrapair fertilization may not play a major role in influencing singing and spatial behaviour in the nightingale: the rate of extrapair fertilization was relatively low (7.5% of the young as indicated by microsatellite genotyping), and males showed no distinct mate guarding activity. In contrast, the probability for a male to stay unpaired was, on average, 33% per year. I suggest that the high singing activity as well as frequent extra-territorial excursions of males after the fertile period of females serve to maintain the own territory and to gather information on other territories and territory occupancy. This information may be vital for defending a good territory and attracting a mate in the current and subsequent breeding seasons.
As only unpaired males sing regularly at night, the proportion of unpaired males can be assessed by comparing the number of nocturnally and diurnally singing males. In an extended study area of 18 km^2, I found that about half of 200 – 240 singing males were unpaired. The male-biased adult sex ratio thus may be a general pattern and play an important role in sexual selection of singing activity and spatial behaviour in the nightingale.

Résumé

J'ai étudié l'activité de chant et le comportement territorial des mâles de Rossignol philomèle afin de déterminer leurs rôles pour attirer une femelle, défendre un territoire, et obtenir ou empêcher des copulations hors couple (« sperm competition »). Les Rossignols mâles chantent de nuit avant l'appariement. Ils s'arrêtent de chanter la nuit dès l'arrivée d'une femelle, mais reprennent leur chant si la femelle les abandonne. Par contre, les mâles non appariés continuent à chanter la nuit tout au long du cycle de reproduction. Ces constats indiquent que le chant de nuit sert à attirer une femelle.

De jour, l'activité de chant est la plus grande pendant l'heure avant le lever du soleil. Ce comportement est largement indépendant du cycle de reproduction et du stade d'appariement, ce qui laisse supposer que, chez le Rossignol, le chant matinal (« dawn chorus ») ne sert pas en premier lieu à attirer une femelle. J'ai vérifié l'alternative que les mâles cantonnés chantent à l'aube pour défendre leur territoire contre des mâles non cantonnés. J'ai transféré des mâles non appariés vers la zone d'étude (la « Petite Camargue Alsacienne ») et j'ai trouvé, par radio-pistage, que, pendant l'heure avant le lever du soleil, ces mâles faisaient des vols de reconnaissance étendus, visitant plusieurs mâles chanteurs, mais, après le lever du soleil, restaient stationnés en dehors des territoires occupés. Ces résultats indiquent que les mâles non cantonnés utilisent le « dawn chorus » pour obtenir des informations sur les mâles chanteurs ou sur l'occupation des territoires. On peut aussi déduire que le chant matinal des mâles cantonnés est important pour marquer l'occupation d'un territoire et le défendre contre des mâles non cantonnés.

En milieu de matinée, contrairement à l'heure avant le lever du soleil, l'activité de chant est fortement influencée par le cycle de reproduction des femelles ; elle est la plus grande pendant les jours de ponte. Il semble que cette grande activité de chant ne serve pas en premier lieu à repousser des mâles cherchant des copulations hors couple en les tenant éloignés des femelles fertiles. En effet, pendant les matinées, quand les pontes ont lieu, les copulations conduisent, de l'avis général, moins facilement à des fécondations que pendant les jours avant le début de la ponte. En conséquence, chez le Rossignol, les distances entre mâles et femelles sont les plus grandes les matins de ponte. Les copulations hors couple n'influencent probablement pas fortement l'activité de chant ni le comportement territorial chez les Rossignol : le pourcentage des jeunes issus d'un autre mâle est relativement faible (DNA-fingerprinting : 7.5 % des jeunes), et les mâles ne surveillent pas intensément les femelles (peu de « mate guarding »). Par contre, la probabilité pour un mâle de rester célibataire pendant la période de reproduction est de 33 % par an. Je suppose qu'une forte activité de chant des mâles ainsi que des reconnaissances fréquentes d'autres territoires après la période fertile des femelles servent à marquer leur propre territoire et à collecter des informations sur d'autres territoires et sur leur occupation. Ces informations pourraient être importantes pour défendre un bon territoire et attirer une femelle lors de la période de reproduction courante ou suivante.

Comme seuls les mâles non appariés chantent régulièrement la nuit, on peut estimer leur pourcentage parmi la population en comparant les nombres de Rossignols chantant la nuit et chantant le jour. Sur une zone d'étude élargie de 18 km^2 autour de la Petite Camargue Alsacienne, j'estime qu'environ la moitié de 200 – 240 mâles chanteurs sont non appariés. Donc, le surplus de mâles adultes pourrait être une situation générale et jouer un rôle important dans la sélection sexuelle du chant et du comportement territorial chez le Rossignol.

Zusammenfassung

Ich untersuchte Gesangsaktivität und Raumverhalten männlicher Nachtigallen im Hinblick auf mögliche Funktionen bei der Anlockung eines Weibchens, der Revierverteidigung und der Konkurrenz um Fremdbefruchtungen („sperm competition"). Männliche Nachtigallen sangen in den Nächten vor der Verpaarung. Nach Ankunft eines Weibchens hörten sie auf, nachts zu singen, fingen aber wieder damit an, falls sie vom Weibchen verlassen wurden. Unverpaarte Männchen sangen dagegen die ganze Brutsaison hindurch nachts. Diese Resultate weisen darauf hin, dass Nachtgesang der Anlockung von Weibchen dient.

Während des Tages war die Gesangsaktivität am höchsten in der Stunde vor Sonnenaufgang. Dieses Muster war weitgehend unabhängig von Brutzyklus und Verpaarungsstatus, was vermuten lässt, dass der Morgengesang („dawn chorus") bei der Nachtigall nicht in erster Linie zum Anlocken eines Weibchens dient. Ich überprüfte die alternative Hypothese, nach der revierbesitzende Männchen in der Stunde vor Sonnenaufgang singen, um ihr Revier gegen revierlose Männchen zu verteidigen: Ich transportierte unverpaarte Männchen in das Untersuchungsgebiet (die „Petite Camargue Alsacienne") und fand mittels Radio-Telemetrie, dass diese Männchen in der Stunde vor Sonnenaufgang ausgedehnte Erkundungsflüge machten und mehrere singende Männchen besuchten, während sie nach Sonnenaufgang stationär und ausserhalb besetzter Reviere blieben. Daraus kann man schliessen, dass revierlose Männchen den „dawn chorus" nutzen, um Informationen über singende Männchen oder über die Revierbelegung zu gewinnen. Es scheint ausserdem, dass der Morgengesang revierbesitzender Männchen wichtig ist, um das Revier zu markieren und gegen revierlose Männchen zu verteidigen.

Im Gegensatz zur Stunde vor Sonnenaufgang war die Gesangsaktivität am Vormittag stark vom Brutzyklus des Weibchens beeinflusst und hatte einen Höhepunkt während der Tage der Eiablage. Diese erhöhte Gesangsaktivität ist jedoch wohl nicht in erster Linie wichtig, um Fremdkopulationen suchende Rivalen abzuschrecken und vom fruchtbaren Weibchen fernzuhalten, da während der Morgenstunden, wenn die Eier gelegt werden, Kopulationen nach allgemeiner Auffassung weniger leicht zur Befruchtung führen als in den Tagen bevor die Eiablage beginnt. Entsprechend hielten sich Nachtigallmännchen in den Morgenstunden der Tage der Eiablage am weitesten entfernt von ihren Weibchen auf. Der Einfluss, den Fremdbefruchtungen auf Gesangsaktivität und Raumverhalten haben, ist bei der Nachtigall wahrscheinlich gering: Der Anteil der Fremdbefruchtungen war relativ klein (Mikrosatelliten-Analyse: 7.5% der Nestlinge), und die Männchen zeigten keine ausgeprägte Partner-bewachung („mate guarding"). Dagegen betrug die Wahrscheinlichkeit, dass ein Männchen unverpaart blieb, im Durchschnitt 33% pro Jahr. Ich vermute, dass die erhöhte Gesangsaktivität der Männchen, ebenso wie häufige Ausflüge in andere Reviere, die nach der fruchtbaren Periode des Weibchens stattfanden, dazu dienen, das eigene Revier zu markieren und Informationen über andere Reviere oder über die Revierbelegung zu gewinnen. Diese Informationen könnten wichtig sein, um in der laufenden oder in nachfolgenden Brutperioden ein gutes Revier zu verteidigen und ein Weibchen anzulocken.

Da nur unverpaarte Männchen regelmässig nachts singen, kann der Anteil unverpaarter Männchen eines Nachtigallenbestandes abgeschätzt werden, indem man die Anzahl nachts singender und tagsüber singender Männchen vergleicht. Für ein erweitertes Studiengebiet von 18 km^2 rund um die Petite Camargue Alsacienne schätze ich, dass etwa die Hälfte der 200 – 240 singenden Männchen unverpaart war. Ein starker Männchen-Überschuss unter den Altvögeln könnte deshalb ein weit verbreitetes Muster sein und eine wichtige Rolle bei der sexuellen Selektion von Gesangsaktivität und Raumverhalten der Nachtigall spielen.

Gesangsaktivität und Raumverhalten
als sexuell selektierte Muster bei der Nachtigall
Luscinia megarhynchos

Einführung, Hauptresultate und Aufbau der Dissertation

„Die Männchen der Singvögel (...) suchen nicht aktiv ein Weibchen, vielmehr beziehen sie im Frühling einen auffälligen Platz und verströmen ihre vollen und sinnlichen Gesänge, die das Weibchen instinktiv kennt und sich zu dem Platze begiebt, um ihr Männchen zu wählen. Mr. Jenner Weir berichtet mir, dass dies sicherlich auf die Nachtigall zutrifft.“
Darwin (1871)

Warum sollte ein Vogel nachts singen statt zu schlafen? Der nächtliche Ruf männlicher Blausturmvögel (*Halobaena caerulea*) dient jagenden Skuas (*Catharacta antarctica*) dazu, ihre Beute, eben männliche Blausturmvögel, zu lokalisieren (Mougeot & Bretagnolle 2000). Nachts singende Nachtigallmännchen verlieren umso mehr Gewicht, je intensiver sie singen (Thomas 2002). Warum also tun männliche Vögel etwas, das nicht direkt mit Nahrungsaufnahme oder Nestlingspflege zu tun hat und die Überlebenschancen offenbar eher schmälert? Charles Darwin (1871) fand, dass solches und ähnliches Verhalten auf den ersten Blick die Weitergabe der eigenen Gene in die nächste Generation gefährdet. Vogelgesang hätte aber kaum Chancen, auf natürlichem Wege selektiert zu werden, wenn er denn nicht auch Vorteile brächte. Darwin schlug deshalb eine Komponente der natürlichen Selektion vor, die Merkmale fördert, welche den Fortpflanzungserfolg unmittelbar steigern, obwohl sie die eigenen Überlebenschancen schmälern. Er nannte diese Komponente die sexuelle Selektion (ausführlicher besprochen in Amrhein 1999a): Männliche Vögel müssen singen, weil die Weibchen anhand des Gesanges ihre Männchen auswählen; die jeweils aus Weibchen-Sicht schöner singenden Männchen vererben demnach den Gesang an ihre zahlreicheren Nachkommen. Männchen singen aber auch im Wettstreit gegen andere Männchen, und der Gewinner bekommt das Revier, das Weibchen und den Fortpflanzungserfolg.

Mag also sein, dass die Vogelmännchen singen, um Weibchen anzulocken. Mr. Jenner Weir (siehe oben) wusste schon zu Darwins Zeiten, dass dies sicherlich auf die Nachtigall zutrifft. Auch in den Handbüchern steht zu lesen, dass vor allem der berühmte Nachtgesang mit der Paarbildung zusammenhängt und zum Anlocken der Weibchen dient (Cramp 1988; Glutz von Blotzheim & Bauer 1988). Bei genauerem Studium der Literatur findet sich jedoch nirgends eine veröffentlichte quantitative Untersuchung des nächtlichen Gesangsverhaltens in Relation zum Verpaarungsstatus. Wenn der Nachtgesang zur Anlockung von Weibchen dient, dann müsste er sofort nach erfolgter Paarbildung aufhören. Während Hilprecht (1965) noch von der Nachtigall vermutet, dass „es Vögel gibt, die mehr am Tage, andere, die mehr in der Nacht schlagen", erwähnt Grüll (1981), dass „Nachtgesang bei jenem Teil der Population, bei dem im Laufe der Brutzeit Verpaarung festgestellt werden konnte, nur innerhalb von 16 Tagen" zu hören war, während Männchen, die bis Ende Mai auch nachts sangen, wahrscheinlich unverpaart geblieben waren. Am Anfang meiner Dissertation stand der Vorsatz, hier „harte Fakten" zu schaffen. Die Daten in **Kapitel I** zeigen, dass Nachtigallmännchen im Untersuchungsgebiet „Petite Camargue Alsacienne" direkt nach der Verpaarung aufhörten, nachts zu singen, während alle unverpaarten Männchen bis zum Ende der Brutsaison nachts weitersangen. Dies lässt vermuten, dass der nächtliche Nachtigallengesang tatsächlich zum Anlocken der Weibchen dient. Kapitel I zeigt ausserdem, dass verpaarte Männchen tagsüber am meisten während genau der Tage sangen, an denen ihre Weibchen Eier legten.

Kapitel II untersucht, zu welchen Tageszeiten dieser Gesangshöhepunkt am ausgeprägtesten war und diskutiert mögliche Funktionen einer solchen verstärkten Gesangsaktivität (diese Hypothesen werden teilweise in Kapitel IV überprüft; siehe unten). Im Unterschied zu anderen Tageszeiten war die Gesangsaktivität in der Stunde vor Sonnenaufgang auch lange nach Eintreffen der Weibchen noch sehr hoch, und zwar sowohl bei unverpaarten als auch bei verpaarten Männchen. Dies lässt vermuten, dass der bekannte Morgenchor der Singvögel vor Sonnenaufgang zumindest bei der Nachtigall nicht in erster Linie zur Anlockung der Weibchen dient. Morgengesang könnte zum Beispiel während der gesamten Brutsaison wichtig sein für die Verteidigung eines Revieres gegen andere Männchen (überprüft im nachfolgend besprochenen Kapitel III).

„White von Selborne (...) fügt hinzu, dass er einen Mann kannte, der glaubte, weibliche Rebhühner würden durch die Kämpfe ihrer Männchen belästigt und letztere deshalb für gewöhnlich schoss; und obwohl er dasselbe Weibchen mehrere Male zur Witwe gemacht hatte, war sie immer sehr bald wieder mit einem frischen Partner versorgt. (...) Ich könnte analoge Fälle hinzufügen, betreffend den Buchfink, die Nachtigall und den Rotschwanz."
Darwin (1871)

Eine der oft zitierten, aber bisher unbestätigten Hypothesen über den frühmorgendlichen Chorgesang ist, dass Vogelmännchen ihre Reviere vor Sonnenaufgang am intensivsten verteidigen müssten, falls revierlose Männchen genau dann ein Revier suchen (Kacelnik & Krebs 1983). Nun ist seit längerem bekannt, dass es in vielen Vogelpopulationen unverpaarte und teilweise revierlose Tiere gibt, sogenannte „floaters", die potentiell eine Gefahr für die Revierbesitzer darstellen (Smith 1978). Wie Charles Darwin zum Bericht des White von Selborne anmerkt, kann man männliche Nachtigallen beliebig oft schiessen, und doch findet sich immer wieder ein neues bisher unverpaartes Männchen ein. In **Kapitel III** zeige ich auf wesentlich unblutigere Art, dass im Jahre 2002 die Hälfte aller Männchen in der Petite Camargue unverpaart war. Die Methodik dafür wurde in den ersten beiden Kapiteln entwickelt: allnächtliche Kontrollgänge zeigen, welche Männchen regelmässig die ganze Brutsaison hindurch nachts singen; dies müssen die unverpaarten Männchen sein. Kapitel III liefert nun die erste Bestätigung der Hypothese von Kacelnik & Krebs (1983) zur Funktion des Morgenchores. Ich fing unverpaarte Männchen 70 km nördlich in der Gegend von Marckholsheim (F) und versetzte sie in die Petite Camargue. Die mit einem Telemetriesender ausgestatteten Männchen blieben tagsüber still sitzen und nutzten exakt die Stunde vor Sonnenaufgang, wenn alle Revierbesitzer sangen, um die Gegend weiträumig zu erkunden, mehrere besetzte Reviere zu besuchen, und auch teilweise ein unbesetztes Revier für sich auszuwählen. Dies bedeutet, dass eine wesentliche Funktion des Morgengesanges die Markierung und Verteidigung des Revieres gegen reviersuchende Männchen sein kann.

Ein Rätsel gab das in Kapitel I und II beschriebene Muster auf, dass verpaarte Nachtigallen tagsüber genau dann am meisten sangen, wenn ihre Weibchen Eier legten. Das könnte damit in Zusammenhang stehen, dass bei Singvögeln durchschnittlich 17.6% aller Jungvögel nicht vom sozialen Partner eines Weibchens abstammen (Wink & Dyrcz 1999), sondern von fremden Männchen gezeugt werden (ausführlicher besprochen in Amrhein 1999a). Verstärkter Gesang nach Ankunft des Weibchens kann laut Møller (1991) die Funktion haben, Nebenbuhler vom fruchtbaren Weibchen fernzuhalten und die eigene Vaterschaft zu verteidigen. In Kapitel I und II stelle ich eine alternative Hypothese auf: Der Gesang während des Eierlegens könnte an das eigene Weibchen gerichtet sein, um dieses von der Qualität des Männchens und damit von der zu erwartenden Qualität der Jungtiere zu überzeugen; die Weibchen könnten dadurch veranlasst sein, mehr kostbare Ressourcen wie Testosteron in den Eidotter zu investieren (Gil et al. 1999). In **Kapitel IV** habe ich diese Hypothese überprüft. Durch Telemetrierung von Nachtigall-Pärchen konnte ich feststellen, dass die Männchen während der Zeit des Eierlegens nicht etwa nahe beim Weibchen sangen, sondern im Gegenteil so weit entfernt sangen wie sonst während des ganzen Brutzyklus nicht. Dies spricht gegen die „Weibchen-Animierungs-Hypothese“ und dafür, dass der Gesang während des Eierlegens eher nach aussen gerichtet ist, zum Beispiel an andere Männchen. Wie nötig ist aber die Abschreckung von Nebenbuhlern und die Verteidigung der eigenen Vaterschaft bei der Nachtigall? In Kapitel IV zeige ich, dass „Fremdvaterschaften“ weitaus seltener vorkamen als zum Beispiel beim nahe verwandten Blaukehlchen (Johnsen et al. 1998), und dass die Nachtigallmännchen auch weit seltener ihr fruchtbares Weibchen bewachten. Die Verteidigung der eigenen Vaterschaft scheint nicht das primäre Ziel von Gesang und Raumverhalten der Nachtigallmännchen zu sein. Hingegen zeigten die verpaarten Männchen ähnliches Verhalten wie die unverpaarten Männchen aus Kapitel III: sie erkundeten fremde Reviere und besuchten brütende, also nicht mehr fruchtbare Weibchen sowie singende Männchen.

„In zahlreichen Fällen scheint es speziell so arrangiert worden zu sein, dass ein Konkurrenzkampf zwischen den Männchen entsteht. Demgemäss kommen bei Zugvögeln die Männchen generell vor den Weibchen im Brutgebiet an, so dass jeweils mehrere Männchen dazu bereit stehen, um jedes einzelne Weibchen zu kämpfen. Die Vogelfänger behaupten, dass dies ausnahmslos auf die Nachtigall zutrifft (...)“
Darwin (1871)

In Kapitel IV stelle ich die Hypothese auf, dass die bereits verpaarten Männchen singen und fremde Reviere erforschen, um sich im Kampf um das eigene Territorium und das eigene Weibchen besser zu positionieren. Ausflüge in fremde Reviere könnten zum Beispiel dazu dienen, die Qualität der Konkurrenten und der anderen Reviere abzuschätzen (Naguib et al. 2004), um in der folgenden Brutsaison ein möglicherweise neues und besseres Revier erfolgreicher zu verteidigen (Doligez et al. 2004). Seit 1997 waren in der Petite Camargue jedes Jahr im Durchschnitt ein Drittel der Männchen unverpaart. Zudem behaupte ich (in Kapitel IV) als Vogelfänger, dass die Männchen bei der Nachtigall generell vor den Weibchen ankamen, sodass nach Charles Darwin ein starker Konkurrenzkampf um jedes einzelne Weibchen entbrennen sollte. Nun ist aber nach Catchpole & Slater (1995) für die längerfristige Bindung eines Weibchens der Besitz eines Revieres die unerlässliche Voraussetzung. Dies ist die Hauptaussage von Kapitel IV: Im Vergleich zu anderen Arten sind bei männlichen Nachtigallen Ausflüge in andere Reviere und das Gesangsverhalten vermutlich weniger mit Verhinderung oder Erlangung von Fremdvaterschaften verbunden, sondern dienen eher der Verteidigung eines Revieres und letztlich der Bindung eines Weibchens.

Was bedeuten diese Resultate für das naturkundliche Alltagsleben? Sie haben das Wissen vermehrt über die biologische Funktion des kulturgeschichtlich vermutlich einflussreichsten Vogelgesanges der Welt (Haag-Wackernagel 1996; Blizzard 2003). Meine Studien haben aber auch Resultate gebracht, die für jeden Vogelkundler und Naturschützer unmittelbar anwendbar sind. Es ist jetzt klar, dass man durch Kontrolle der nächtlichen Gesangsaktivität feststellen kann, ob ein Nachtigallmännchen verpaart ist oder nicht. **Kapitel V** zeigt die Bedeutung dieser Frage für den Naturschutz auf. Im Frühjahr 2003 haben wir auf einer Fläche von knapp 18 km^2 rund um die Petite Camargue den Bestand singender Nachtigallen gezählt. Die Ergebnisse dieser Kartierung wurden bei den Planungsarbeiten zur Erweiterung des Naturschutzgebietes „Petite Camargue Alsacienne" berücksichtigt (P. Knibiely, mündl. Mitt.; siehe Allgemeine Methoden). Unsere Zählung war nicht nur eine der grösstflächigen je durchgeführten Nachtigallkartierungen, sondern meines Wissens auch die erste grossflächige Singvogelkartierung, bei der nicht nur die Anzahl singender Männchen, sondern auch deren Verpaarungsstatus festgestellt wurde. Von den 200 – 240 singenden Männchen waren etwa die Hälfte unverpaart. Das bedeutet, dass nicht jede singend angetroffene Nachtigall Junge im Nest hat und deswegen eine Erfolgsmeldung für den Artenschutz ist. In den direkt südlich des Zählgebietes liegenden Kantonen Basel-Landschaft und Basel-Stadt sind seit den dreissiger Jahren des 20. Jahrhunderts nur vereinzelte Nachtigallen zu hören gewesen (Blattner & Kestenholz 1999). In Aesch (BL) sang eine Nachtigall vom 25.4. bis zum 31.5. 2002, und „derart lange Aufenthalte lassen Brutverdacht aufkommen" (Blattner & Veszeli 2002). Haben solche Einzelsänger eine Chance, ein Weibchen anzulocken und vielleicht den Grundstein für eine sich neu ansiedelnde Population zu legen? Die eifrigsten Sänger, auch solche, die den ganzen Mai hindurch zu hören sind, haben leider oft kein Weibchen. Wer es genau wissen will, kann einen schönen Abend zu Beginn der zweiten Maihälfte aussuchen, bis 11 oder 12 Uhr nachts abwarten, und hoffen, dass die Nachtigall nicht zu singen anfängt (weil sie sonst eben wahrscheinlich unverpaart ist).

Ausblick

Die Nachtigallforschung in der Petite Camargue wird fortgesetzt. Für das Jahr 2004 haben sich bereits InteressentInnen für ein Doktorat im Nachtigallprojekt angemeldet. Was gibt es noch zu erforschen? Die Antwort könnte sein: Soviel wie über die Taufliege, den Zebrafinken oder den Menschen. Wodurch entscheidet sich, welches Männchen ein Weibchen anlocken kann und welches nicht? Ist im Nachtgesang die „Qualität“ der Männchen codiert, oder wählen die Weibchen eher nach der Qualität der Reviere? Was ist ein gutes Revier? Führen Revierwechsel unverpaarter Männchen zum Verpaarungserfolg im nächsten Jahr? Wodurch kommt der starke Männchen-Überschuss unter den Altvögeln zustande? Nicht zuletzt: Was können wir tun, damit wir wenige Kilometer südlich der Petite Camargue in den Kantonen beider Basel wieder mehr singende Nachtigallen hören, die möglichst bald nach der Ankunft nachts schlafen statt um ein Weibchen zu singen?

Diese Dissertation hat hoffentlich den Grundstein gelegt für eine weiterhin erfolgreiche Zusammenarbeit mit *Luscinia megarhynchos*.

Allgemeine Methoden

Untersuchungsgebiet und Forschungsstation

Die Petite Camargue Alsacienne liegt im Oberrheintal in Frankreich, etwa 8 km nord-nordwestlich von Basel (Abb. 1), auf 240 – 250 m ü.M. im ehemaligen Überschwemmungsgebiet des Rheins (Gallusser & Schenker 1992). Die Landschaft ist ein Mosaik aus Bruchwäldern, Buschwerk, Schilf, Wiesen und künstlichen Fischteichen, die heute, gut 150 Jahre nach ihrer Entstehung (Binnert 1999), den Habitus natürlicher Wasserflächen haben (eine detaillierte Karte des Untersuchungsgebietes findet sich im Anhang). Die nördliche Hälfte des Gebietes (ca. 120 ha) ist seit 1982 staatliches Naturschutzgebiet. Die südliche Hälfte der Petite Camargue ist das eigentliche Untersuchungsgebiet (ca. 120 ha; Abb. 1) und steht zum Zeitpunkt dieser Dissertation noch nicht unter offiziellem Naturschutz; eine Erweiterung des Schutzgebietes auf dieses Areal und weit darüber hinaus steht aber unmittelbar bevor. Das gesamte Gebiet wird gepflegt und verwaltet vom trinationalen Verein „Petite Camargue Alsacienne“ (Direktor: Philippe Knibiely).

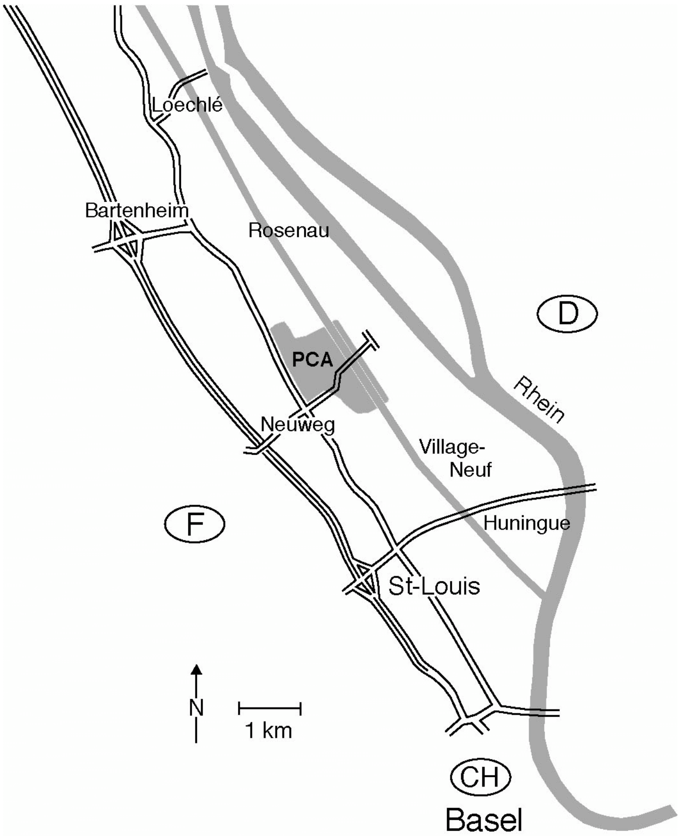

Abb. 1. Lage des Untersuchungsgebietes Petite Camargue Alsacienne (PCA)

In den zentral gelegenen Gebäuden der „Kaiserlichen Fischzucht“ (gegründet 1852; Binnert 1999) befindet sich unter anderem die „Forschungsstation Petite Camargue Alsacienne“, die 1989 unter der Leitung von Prof. Heinz Durrer eingerichtet wurde und der Universität Basel angegliedert ist (Durrer 2001). Die Forschungsstation war seit ihrer Gründung federführend bei umfangreichen Renaturierungsarbeiten in grossen Teilen der Petite Camargue (Durrer 1997); diese Aufgaben sind inzwischen vom Verein Petite Camargue Alsacienne übernommen worden. Die Forschungsstation wird getragen von der „Association Suisse Pro Petite Camargue Alsacienne“, einem privaten Förderverein unter der Präsidentschaft von Helmut Hersberger.

Forschungsprojekt „Nachtigall“

Das Forschungsprojekt „Nachtigall“ wurde 1994 von H. Durrer initiiert und begann mit Revierkartierungen (durch F. Buner und C. Rivera), deren Ergebnisse 1995 veröffentlicht wurden (Durrer et al. 1995). Ab 1996 habe ich die Revierkartierungen fortgeführt und ab 1997 mit der Beringung der Nachtigallen begonnen. 1998 fing ich an, zunächst einzelne Weibchen mit Telemetrie-Sendern zu versehen (siehe unten). Erste Resultate hierzu finden sich in der Diplomarbeit (Amrhein 1999b). Ein wesentlicher Teil meiner wissenschaftlichen Bemühungen bestand fortan im Aufbau einer Nachtigall-Forschungsgruppe (Tab. 1). Ein wichtiger Schritt hierzu war, dass ich im Jahre 2001 PD Dr. Marc Naguib von der Universität Bielefeld dafür gewinnen konnte, seine Feldarbeit von Berlin an unsere Forschungsstation zu verlegen. Seither bestreiten wir die Feldsaison gemeinsam mit seinem Doktoranden Hansjörg Kunc und hatten zwei Nachtigall-DiplomandInnen sowie jedes Jahr bis zu fünf langfristig anwesende FeldassistentInnen aus verschiedenen Ländern (Tab. 1). Die Arbeit wurde finanziert von der Association Suisse Pro Petite Camargue Alsacienne, der Deutschen Forschungsgemeinschaft und der Universität Bielefeld; für die Jahre 2002 und 2003 konnte ich ausserdem die grosszügige Unterstützung der Stiftung Emilia Guggenheim-Schnurr der Naturforschenden Gesellschaft in Basel gewinnen.

Tab. 1
Das Nachtigallprojekt 1997 – 2003
Arbeitsschwerpunkte und
TeilnehmerInnen mit mehrwöchigem Aufenthalt (Herkunftsland)

1997	1998	1999	2000	2001	2002	2003
Revierkartierung Beringung	Revierkartierung Beringung Blutproben Telemetrie Weibchen	Revierkartierung Beringung Blutproben Telemetrie Weibchen	Revierkartierung Beringung Blutproben Telemetrie Weibchen Gesangs-Playback	Revierkartierung Beringung Blutproben Telemetrie Weibchen Telemetrie Männchen Gesangs-Playback Gesangsaufnahmen	Revierkartierung Beringung Blutproben Telemetrie Weibchen Telemetrie Männchen Gesangs-Playback Gesangsaufnahmen Männchen-Versetzung Parasitenuntersuchung	Revierkartierung Beringung Blutproben Telemetrie Weibchen Telemetrie Männchen Gesangs-Playback Gesangsaufnahmen
V. Amrhein	V. Amrhein M. Lutsch (F)	V. Amrhein M. Lutsch (F) D. Matti (CH)	V. Amrhein M. Lutsch (F) G. Stephinger (D)	V. Amrhein M. Lutsch (F) M. Naguib (D) H. Kunc (A) M. Brandt (D) C. Tennie (D)	V. Amrhein M. Lutsch (F) M. Naguib (D) H. Kunc (A) B. Benzing (D) C. Herhausen (D) M. Weerheim (NL) H. Altrichter (D) C. Eikenaar (NL) G. Kraus (D)	V. Amrhein M. Lutsch (F) M. Naguib (D) H. Kunc (A) S. Michler (CH) A. Selbach (D) B. Szelényi (H) R. Schmidt (D)

Revierkartierung und Gesangsaktivität

Seit Beginn meiner Nachtigallforschung habe ich versucht, den wichtigsten Standortvorteil der Forschungsstation möglichst effektiv auszunutzen: sie befindet sich inmitten einer Nachtigallenpopulation von bis zu 50 Revieren (Durrer et al. 1995). Seit 1997 werden zur Brutzeit täglich mehrere Rundgänge durch das Gebiet gemacht, und zwar über den ganzen Tag verteilt, einschliesslich einer nächtlichen Runde um Mitternacht. Diese Rundgänge dienen zunächst dazu, die Orte zu kartieren, an denen die Männchen singen, und damit die Gesangsreviere zu definieren. Die Rundgänge werden nach einer genau festgelegten Methode durchgeführt (gleicher Weg, gleiche Zeitdauer, abwechselnde Wegrichtungen) und bieten sich damit auch als Mittel an, die Gesangsaktivität der Männchen als Prozentsatz der Kontrollen mit Gesang zu quantifizieren. Diese Methode wurde im Prinzip schon von Grüll (1981) für die Nachtigall eingeführt. Er kommt jedoch zu völlig anderen Ergebnissen; zum Beispiel findet er eine der niedrigsten Gesangsaktivitäten während der Eilege-Periode (vgl. Einführung und Kapitel I und II). Eine der Ursachen für diese Unstimmigkeit mag darin liegen, dass Grüll die Methode in drei von vier Jahren seiner Untersuchung nicht anwandte, sondern den subjektiven Eindruck der Gesangsintensität eines Vogels in Prozentzahlen umrechnete, um die Daten aller vier Jahre zusammen auswerten zu können (Grüll 1981, Seite 261).

Die Gesangsaktivität, definiert als der Prozentsatz der Beobachtungseinheiten, bei denen ein Vogel singt, ist meines Wissens bei keiner Vogelart so konsequent über Jahre hinweg erfasst worden wie in der vorliegenden Studie. Die Gesangsaktivität als quantitatives Mass für den Taggesang und als qualitatives Mass für den Nachtgesang ist das Hauptthema der ersten beiden Kapitel. Insbesondere die Erfassung der nächtlichen Gesangsperioden ist aber die Grundlage für das gesamte Forschungsprojekt.

Fang und Beringung

Frankreich trägt die Verantwortung für den grössten europäischen Nachtigallenbestand von gut 1 Million Brutpaaren (Hagemeijer & Blair 1997; Deutschland: 100'000, Schweiz nach Schmid et al. 1998: 2000 – 2500). Die Nachtigallberingung ist ein nationales Schwerpunktprogramm der Französischen Vogelwarte „Centre de Recherches sur la Biologie des Populations d'Oiseaux” in Paris. Im Rahmen dieses Programms habe ich 1997 unter Anleitung von Henri Jenn (dem Leiter der elsässischen Vogelberingung) begonnen, Nachtigallen in den Revieren unseres Untersuchungsgebietes zu fangen. Dazu habe ich vor

Sonnenaufgang pro Tag insgesamt ca. 10 Netze aufgestellt, verteilt auf ca. 3 Reviere (Abb. 2; die meisten Netze mit 6 m Länge, einzelne mit 9 m und 12 m Länge). Als gute Netzstandorte erwiesen sich das Innere von bei Nachtigallen beliebten Buschgruppen oder als Flugschneisen genutzte Bereiche zwischen den Büschen. Die Netze blieben bis maximal 09.00 Uhr offen, oft jedoch fingen sich die Nachtigallen bereits kurz vor oder nach Sonnenaufgang. Die Nachtigallen wurden direkt nach dem Fang vermessen (Alter, Geschlecht, Flügellänge, Tarsuslänge, Gewicht), beringt (1 Metallring und bis zu drei Farbringe) und gegebenenfalls besendert (siehe unten). Alle Individuen anderer Arten wurden sofort nach dem Fang freigelassen. Von 1997 – 2003 habe ich insgesamt 319 Nachtigallen beringt, davon 141 Jungvögel und 178 Altvögel. Die Auswertung dieser Fangdaten ist jedoch nicht Schwerpunkt dieser Dissertation; der Zweck der Beringung lag für mich bisher vor allem in der individuellen Markierung der Tiere, an denen ich Verhaltensstudien durchführte.

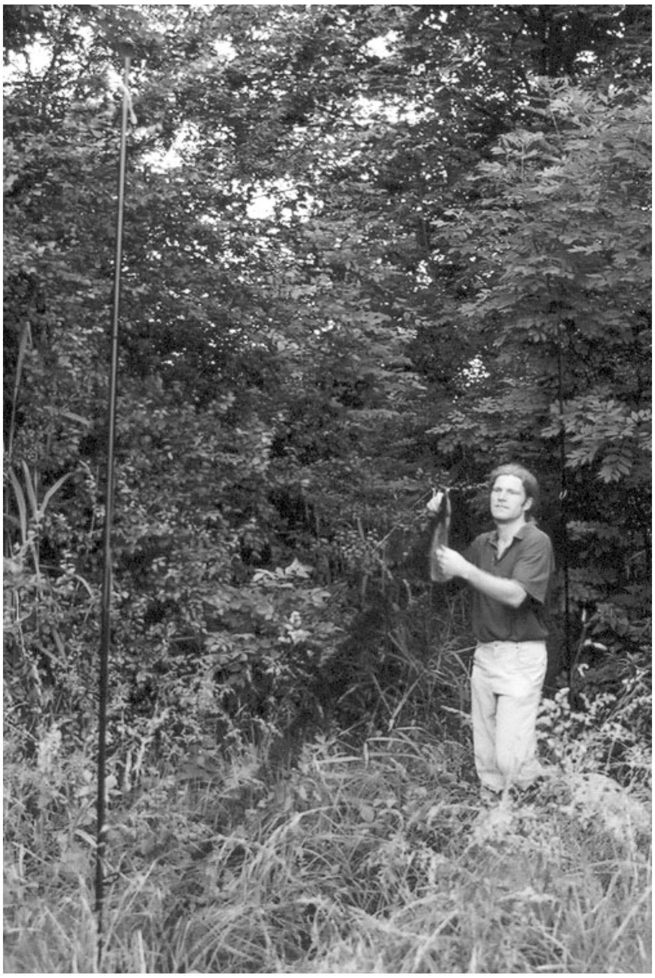

Abb. 2. Aufstellen eines Netzes im Nachtigallrevier

Die Jungvögel wurden zwischen dem 7. und 9. Tag nach dem Schlüpfen im Nest beringt. Von allen Jungvögeln und ihren Eltern nahm ich Blutproben (Kapitel IV). Dafür habe ich nach der allgemein üblichen Methode mit einer sterilen Nadel in die Flügelvene gestochen, den austretenden Blutstropfen in einem Kapillarröhrchen aufgenommen, und die Einstichstelle bis zur Stillung einer eventuell auftretenden Blutung mit medizinischer Watte bedeckt. Die Nester wurden in einigen Fällen durch Beobachten der fütternden Altvögel gefunden. Besonders in dichten Brennessel-Beständen war es jedoch unmöglich, die Nester der bodenbrütenden Nachtigall auf diese Weise zu entdecken. Die schnellste und für die Brut gefahrloseste Methode war meist die Ortung des auf dem Nest sitzenden Weibchens per Radiotelemetrie. Die Nester wurden nach Möglichkeit nur zweimal aufgesucht: beim Finden des Nestortes und bei der Beringung der Jungvögel.

Besenderung

Bei einem Teil der gefangenen Tiere habe ich einen Telemetrie-Sender auf dem Rücken befestigt (Abb. 3). Ich benutzte eine Telemetrie-Ausrüstung von Titley Electronics, Australien (Kapitel III und IV). Die Sender wurden mit einem Rucksack befestigt, dessen zwei Schlaufen um die Beine lagen, so dass der Sender auf dem Rücken etwas oberhalb der Bürzeldrüse zu liegen kam (Rappole & Tipton 1991). Die Sender wogen ca. 0.9 g, was etwa 4.1 – 4.3% des Gewichtes einer Nachtigall entspricht; sie lagen damit deutlich unter der empfohlenen maximalen Zusatzladung von 5 – 7% des Körpergewichtes für Kleinvögel (Naef-Daenzer 1993). Ich kann nicht ausschliessen, dass der Sender das Verhalten der Tiere in der einen oder anderen Weise beeinflusst hat. Jedoch fiel mir in keinem Fall eine Verhaltensänderung nach der Besenderung auf. Die Männchen flogen nach Besenderung meist geradewegs in den nächsten Busch und liessen einige Gesangsstrophen hören, und auch die Weibchen zeigten keine Veränderung im Flugverhalten. In keinem Fall hat ein sesshafter Altvogel selbst nach wiederholtem Fang sein Revier verlassen. Nach Ablauf der Batterie-Lebensdauer (25 – 30 Tage) habe ich die Tiere wiedergefangen und die Sender entfernt; auch beim Wiederfang waren keine durch die Sender verursachten Schürfstellen oder Wunden zu finden. Es gibt einige Studien, die mögliche Verhaltensänderungen bei Singvögeln nach Befestigung von Sendern mit der von mir benutzten Rucksack-Methode untersucht haben. Kapuzenwaldsänger (*Wilsonia citrina*) mit Sendern, die 7 – 8.5% des Körpergewichtes der Vögel wogen, zeigten keine Veränderung im Brutverhalten: Fütterungsrate und Bebrütungsdauer waren gleich wie bei nicht-besenderten Tieren (Neudorf & Pitcher 1997).

Walddrosseln (*Hylocichla mustelina*), bei denen die Sender (4% des Körpergewichtes) vor dem Wegzug ins Winterquartier nicht abgenommen worden waren, zeigten keine erhöhte Sterblichkeit während des Zuges und verloren nicht mehr Gewicht als unbesenderte Vögel (Powell et al. 1998). Die Autoren empfehlen deshalb den fortgesetzten Gebrauch der Befestigungs-Methode nach Rappole & Tipton (1991) und sind „überzeugt, dass unsere Sender (...) keinen offenkundigen negativen Effekt auf damit markierte Walddrosseln hatten.“

Abb. 3. Besenderte Nachtigall

Danksagung

Prof. Dr. Heinz Durrer verdanke ich langjährige Unterstützung und die einmalige Gelegenheit, in der Petite Camargue Alsacienne arbeiten und mitten in meiner Studienpopulation mit Frau und Kind wohnen zu dürfen.

Ich danke Prof. Dr. Bruno Baur, der als Referent und Fakultätsvertreter den Abschluss meiner Doktorarbeit organisierte.

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An der Schweizerischen Vogelwarte Sempach danke ich Prof. Dr. Bruno Bruderer, Dr. Beat Naef-Daenzer und Dr. Christian Marti für Diskussionen, Koreferat und Hilfe bei der Literatursuche.

Hansjörg Kunc war mein Mit-Doktorand und Mit-Bewältiger der zahlreichen Herausforderungen, die eine Feldsaison mit vielen Nachtigallen und FeldassistentInnen sowie die resultierende Datenflut zu bieten haben.

Pius Korner beriet mich in statistischen Fragen und kommentierte geduldig alle meine Manuskripte sowie auch die meisten anderen Aspekte der Weltgeschichte.

Ohne die Mitarbeit der in Tabelle 1 aufgeführten Personen sowie vieler weiterer kurzfristig anwesender HelferInnen wäre diese Arbeit nicht möglich gewesen. Stellvertretend für sie alle danke ich Martin Lutsch, der mir von 1998 bis heute jede Feldsaison geholfen hat.

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Der Förderverein Association Suisse Pro Petite Camargue Alsacienne finanzierte mich und meine Forschung. Dem Präsidenten Helmut Hersberger und den geschätzten Mitgliedern des Vereins meinen herzlichen Dank für das bis heute und hoffentlich auch in Zukunft entgegengebrachte Vertrauen.

Der Stiftung Emilia Guggenheim-Schnurr der Naturforschenden Gesellschaft in Basel vielen Dank für die substanzielle Unterstützung meiner Arbeit in den Jahren 2002 und 2003.

Susanne und Linn danke ich dafür, dass sie, obwohl sie jetzt gerade wieder einen Sonntag ohne mich verbringen müssen, vermutlich trotzdem heute abend noch guter Laune sind.

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Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle

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This study on the nightingale, *Luscinia megarhynchos*, is the first to examine both nocturnal and diurnal singing activity of mated and unmated males throughout a species' entire breeding cycle. Nocturnal song was sung mostly by unmated males. After pair formation, males ceased nocturnal singing and resumed it if their mate deserted. These results strongly suggest that nocturnal song of unmated males functions to attract a mate. Diurnal singing activity before females settled was low and did not predict future mating status. However, unmated males showed a continuous increase in diurnal singing activity until the end of the breeding cycle, but diurnal singing activity of mated males decreased after the egg-laying period. Mated males resumed nocturnal song for, on average, 3 nights during egg laying by their mates. This second period of nocturnal song coincided with the peak of diurnal singing activity. Such a high male singing effort during egg laying might allow the female to adjust her reproductive effort to male quality, deter rival males (e.g. through honest announcement of the female's fertility) or attract females for extrapair copulations.

Bird song has evolved under both inter- and intrasexual selection (Catchpole & Slater 1995). The males' song may attract and stimulate females and may repel rival males (Kroodsma & Byers 1991), but the importance of these functions may differ between species and between different songs within a species. In several bird species, males change their singing behaviour after mating. Here, song is often regarded as intersexual communication. For instance, reduced singing activity after pair formation indicates that song plays a role in mate attraction (Catchpole 1973; Hanski & Laurila 1993; Gil et al. 1999a). In species in which males use several song patterns, specific patterns may be particularly important to attract females. These patterns may be produced less frequently or even be abandoned after pairing, while the output of other song patterns continues until later stages of the breeding cycle (Hasselquist & Bensch 1991; Nemeth 1996; Staicer 1996). Song sung at different times of the day may also serve different functions. For example, the dawn chorus of male songbirds has been suggested to differ functionally from song at other times of the day (Staicer et al. 1996).

About 10 western Palaearctic species of songbirds are known to sing regular nocturnal song in addition to diurnal song (genera *Acrocephalus*, *Cettia*, *Locustella*, *Luscinia*, *Phoenicurus*; Glutz von Blotzheim 2001), providing particularly suitable species to study changes in song function with time of day. Male nightingales, *Luscinia megarhynchos*, are renowned for high nocturnal singing activity, and their nocturnal song is thought to attract nocturnally migrating females (Cramp 1988; Glutz von Blotzheim 1988). The extensive nocturnal singing is in addition to diurnal song, and there are indications that it is energetically costly (Thomas 2002). Nocturnal song might therefore be an honest signal of male quality on which females could base their mating decisions (Catchpole & Slater 1995). However, empirical evidence on the intersexual function of nocturnal song is still lacking. Until now, most studies of nocturnal song have concentrated on intrasexual communication and it has been shown that male nightingales use multiple singing strategies when interacting with rival males at night (Hultsch & Todt 1982; Naguib 1999; Todt & Naguib 2000). In the nonpasserine corn crake, *Crex crex*, the

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incidence of nocturnal song by males is reduced during pairing (Tyler & Green 1996). Some authors have suggested that nocturnal singing is confined to unpaired males in *Acrocephalus* warblers (Catchpole 1973; Kelsey 1989). However, to date, there is no quantitative evidence in passerines that nocturnal song is related to mating status.

Many songbird species, including the nightingale, sing diurnal song beyond pair formation (Catchpole & Slater 1995). After pair formation, diurnal song could function to attract additional social mates (Hasselquist & Bensch 1991) or to attract neighbouring females for extrapair copulations (Birkhead & Møller 1992; Hasselquist et al. 1996). Prolonged singing may also allow a female to reassess her mate's quality for differential reproductive allocation (Gil et al. 1999b; Sheldon 2000). Furthermore, diurnal song may repel neighbouring males (Nowicki et al. 1998; Naguib et al. 2001). Møller (1991) suggested that a male's elevated singing activity after pairing honestly announces the fertility of his mate and thereby signals his ability to defend paternity (but see Gil et al. 1999a). All these hypotheses predict a peak of singing activity in mated males when females are fertile. So far, no study has examined the singing activity of unmated males for all the corresponding periods of the breeding cycle in mated males. However, a comparison of the singing behaviour of unmated and mated males may hold clues to understanding the functions of song after settlement of females.

In this study, by correlating the incidence of nocturnal song with mating status we tested the hypothesis that, in the nightingale, nocturnal song serves to attract a mate. To identify other possible functions of nocturnal and diurnal song, we correlated the singing activity of mated and unmated males with all the stages in the reproductive cycle.

METHODS

Study Site and Species

We conducted the study from 1998 to 2001 at the Petite Camargue Alsacienne in France, 10 km north of Basel, Switzerland. The area comprises a 1-km^2 mosaic of riverine forest, pastures, fields, reeds and artificial lakes. A dense population of about 50 singing nightingales has been monitored since 1994 (Durrer et al. 1995; Amrhein 1999). The owners of 28 territories and their mates have been regularly colour-ringed since 1997.

Nightingales form socially monogamous seasonal pair bonds. Arrival of the first males at the study site varied between years from 3 to 13 April. The first females were captured 1–3 weeks later. The typical clutch size was five (N=21 of 28 females). Other clutch sizes were three (N=1), four (N=5) and six (N=1). Females laid one egg per day, between 0800 and 1100 hours (N=5 females observed). Replacement clutches were initiated when the brood failed because of predation or inundation, but true second clutches did not occur. Male nightingales sing at dawn and throughout the day. Nocturnal singing usually starts before midnight and continues until dawn.

General Methods

During the breeding season (April–June), we captured males and females in mist nets in up to 19 territories per year. The birds were ringed in their territory and released within 15 min of capture. We performed mist netting for 1 h per day until we had captured both members of a pair, or until we were sure that no female was present in a male's territory. This occasionally resulted in capturing an individual more than once. However, no bird deserted its territory after capture. Furthermore, we have no indications that capturing influenced breeding success or negatively affected other bird species.

We refer to the period from the day a female settled in a male's territory until the day before the first egg was laid as the prelaying period (5–11 days, $\bar{X} \pm \mathrm{SD}=8 \pm 2$, N=19). We defined laying period as the period from the day the first egg is laid to the day before the last egg is laid (usually 4 days). Prelaying and laying periods are usually regarded as the time when females are fertile (Birkhead & Møller 1992). The incubation period is 13 days, the nestling period 11 days (Glutz von Blotzheim 1988) and the fledgling period 16 days (Cramp 1988).

We use the term 'bachelors' for males that remained unpaired throughout the season to avoid confusion with the 'unpaired' period of all males before the arrival of females. To compare the singing activity of bachelors with that of mated males, we divided the season for bachelors into the same periods as for their immediate mated neighbours. For mated males, we considered singing activity only for successful first clutches. All mated males were of known identity and were included in the analyses only once. Five of 12 bachelors were ringed; for the remaining seven birds, we avoided pseudoreplication by sampling each territory only once.

Nocturnal Song

From arrival of the first males until early in June we censused nocturnal song as either present or absent between midnight and 0200 hours. This is the time that most nocturnally singing males sing, and song lasts up to several hours. Therefore, we were likely to encounter a bird singing at this time if it was engaged in nocturnal singing that night. Rounds were made nightly in 2000 and 2001. In 1998 and 1999, rounds were made less frequently towards the end of the breeding cycle (every third to fifth night). The sample consisted of 18 mated males and 12 bachelors.

Diurnal Song

To quantify diurnal singing activity throughout the season, we censused diurnal song as present or absent on one to seven rounds per day ($\bar{X} \pm \mathrm{SD}=3 \pm 2$). Singing activity of a male is expressed as the proportion of rounds on which it was heard singing. The duration of rounds was held constant and, to avoid bias on a particular time of day, we varied the time of the rounds from day to day, covering all hours of daylight. We excluded males if data were not available for all periods of the breeding cycle.

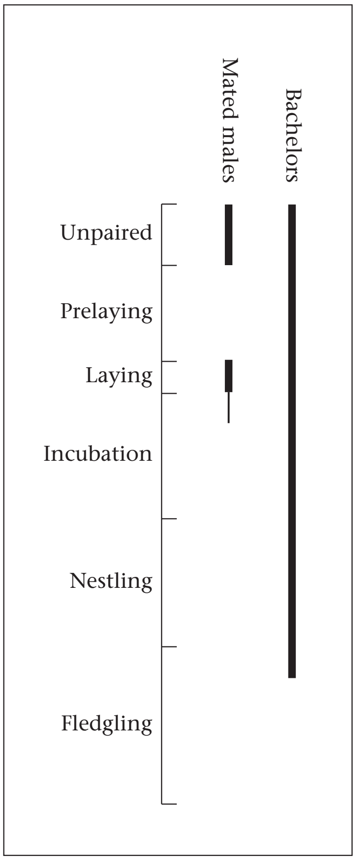

Figure 1. Schematic presentation of nocturnal singing activity in male nightingales over six periods of the breeding cycle. Nocturnal song was censused as present versus absent between midnight and 0200 hours. The indicated periods of song and of breeding activity correspond to mean values for 18 mated males and 12 bachelors. The thin line indicates that only a few mated males continued singing after the laying period.

The final sample included nine mated males and 10 bachelors.

Statistics

All sample sizes refer to the number of individuals; all tests are two tailed. Descriptive statistics in the text are given as ranges and mean ± SD. Proportional data were normalized using an Anscombe transformation (Zar 1996). We used GLM repeated measures procedures with SPSS V.10 for Macintosh.

RESULTS

Nocturnal Song Before Pairing

Of 18 males that attracted a female, 16 were engaged in nocturnal singing before pairing for 1–18 nights (6.0 ± 5.7; Fig. 1). As counted from the last night on which a male sang, we captured a female in his territory the next morning (day 0) to 2 days later (0.7 ± 0.8 days, $N=12$; in four cases, we did not mist-net during the prelaying period). We never observed or captured a female before the male stopped singing at night. Thus, all 12 males stopped singing at night after a female had settled in their territory.

Two males stopped nocturnal singing after a female arrived in their territory, but resumed when the females disappeared. One of the females returned after 2 days, and the male again ceased nocturnal singing. Another male resumed nocturnal singing during the nestling period after its mate had died. A fourth male resumed nocturnal song after its mate had disappeared following predation of the brood, but ceased nocturnal singing again after a new female had settled in his territory.

Nocturnal Song After Pairing

For 15 mated males, we were able to examine whether they resumed nocturnal singing in later stages of the breeding cycle. Of these males, 13 resumed nocturnal singing once the females started egg laying.

Nine of these mated males were sampled every night during the laying period (4 days). They sang for 1–4 nights (2.8 ± 1.4; Fig. 1). Of 12 males for which we have information on the onset of nocturnal song, five resumed singing the night before the first egg was laid, four resumed singing before the second, two before the third, and one before the fourth egg was laid. After egg laying, three of 10 regularly censused males continued singing during the first nights of incubation for 2, 3 and 6 nights (Fig. 1).

For 11 males, we could examine whether nocturnal song during the laying period was closer to egg laying of their mate than to egg laying of neighbouring females. In the neighbouring territories, egg laying started from 7 days earlier to 7 days later than in the focal territories. The 11 focal males resumed nocturnal song significantly closer to the day when their mate laid the first egg (0.8 ± 0.6 days) than to the day when neighbouring females laid their first egg (3.9 ± 2.4 days; Wilcoxon signed-ranks test: $T=2$, $N=11$, $P<0.005$). Furthermore, the onset of nocturnal song was not related to the prelaying period of neighbouring females, since only five of the 11 males resumed nocturnal song before the first egg was laid in neighbouring territories.

Nocturnal Song of Bachelors

To monitor the mating status of males that continued singing at night throughout the breeding season, we regularly performed mist netting in four of these territories. Here, females were never captured nor observed. We considered these males, as well as eight additional males which were never seen with a female, as having remained unpaired. These 12 bachelors were engaged in nocturnal singing over 28–53 nights (38 ± 9; Fig. 1). On average, they stopped singing at night 4 days after the mean fledging date (Fig. 1).

Diurnal Song of Mated Males and Bachelors

Males sang diurnal song throughout the breeding season (Fig. 2). The overall diurnal song output differed

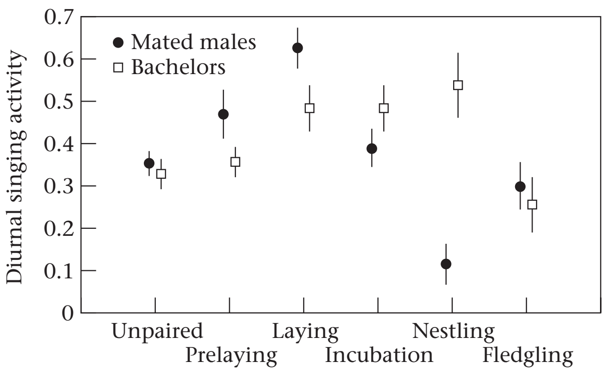

Figure 2. Mean±SE diurnal singing activity of male nightingales over six periods of the breeding cycle, based on 3±2 ($\bar{X}$±SD) rounds per day conducted on the study site throughout the breeding season. Singing activity of a male is expressed as the proportion of rounds on which it was heard singing. The time periods for bachelors (N=10) were determined by the breeding periods of their closest mated neighbours (N=9 mated males).

between periods of the breeding cycle (GLM repeated measures: $F_{5,85}=7.72$, $P<0.001$), but not between mated males and bachelors ($F_{1,17}=1.13$, $P=0.30$). However, the interaction between mating status and periods of the breeding cycle was significant ($F_{5,85}=9.16$, $P<0.001$), suggesting that seasonal changes in diurnal singing activity differ between bachelors and mated males.

Before arrival of the females, all males started with diurnal singing activity at an intermediate level, and singing activity did not predict later mating status (t test between mated males and bachelors for the unpaired period: $t_{17}=-0.66$, $P=0.52$; Fig. 2). However, during the laying period, mated males sang more than bachelors, although this was marginally nonsignificant ($t_{17}=-2.096$, $P=0.051$).

For bachelors, a separate repeated measures GLM revealed differences in diurnal singing activity between periods of the breeding cycle ($F_{5,45}=4.39$, $P=0.003$). The singing activity of bachelors increased until the nestling period (from the unpaired period until the nestling period, the linear term of the repeated measures GLM was significant: $F_{1,9}=7.83$, $P=0.021$).

In mated males, too, diurnal singing activity differed between periods ($F_{5,40}=12.99$, $P<0.001$). Mated males had their highest song output during the laying period. They sang least during the period of feeding nestlings. In mated males, diurnal singing activity in the laying period differed significantly from that of the unpaired, nestling and fledgling periods (Bonferroni-adjusted post hoc multiple comparisons: all $P<0.02$).

DISCUSSION

Our study provides the first quantitative evidence in songbirds that nocturnal song is related to mating status. Male nightingales ceased nocturnal singing with pair formation and resumed it if their mate deserted. Furthermore, males that remained unmated continued to sing at night until the end of the breeding season. These results strongly suggest that a main function of nocturnal song is mate attraction. We also found that diurnal singing activity before the settlement of females was comparatively low and did not predict future mating status. This observation may indicate that singing during the day is less important for mate attraction in the nightingale.

Low background noise at night makes nocturnal song particularly suitable for long-distance advertisement to migrating females (Wiley & Richards 1982). Since sound transmission is better at night than in the day, nocturnal song might preferably be used by females to assess differences in male singing traits. If nocturnal song is costly (Thomas 2002), the advertisement through nocturnal singing may be an honest signal reflecting male quality.

The increase in diurnal singing activity after the arrival of females might have resulted from changing environmental conditions such as increased temperature and food availability (Gottlander 1987). However, such a causal relationship does not explain the observed fluctuations in singing activity of mated males. Males may sing in the day throughout the season to repel other males (Nowicki et al. 1998). Indeed, male nightingales with high diurnal song rates suffered from fewer territorial intrusions by neighbouring males than did males with lower song rate (Naguib et al. 2001). The greater increase in diurnal singing activity until the end of the laying period in mated males than in bachelors is in line with this intrasexual function of diurnal song, because mated males may be especially vulnerable to intrusions from other males seeking extrapair copulations.

Mated males resumed nocturnal singing when their mates laid eggs. This resumption of nocturnal song coincided with the peak of diurnal singing. Because diurnal song has been shown to repel rival males, and we found that nocturnal song functioned to attract females, it is possible that the high overall singing activity during egg laying serves both intrasexual and intersexual functions. It is, however, unlikely that during egg laying, nocturnal song serves to attract additional social mates. We never observed true cases of simultaneous polygyny, nor are these reported in the literature. Nevertheless, this second period of nocturnal song may serve other intersexual functions. An increase in song output of mated males during the fertile time of their mates is also known for other species, and there are several mutually nonexclusive hypotheses to explain this phenomenon.

We found that the onset of the second period of nocturnal song was linked to the mate's egg laying and not to that of neighbouring females. This suggests that the breeding behaviour of his mate is the primary factor determining a male's decision to resume nocturnal song. One functional explanation could be that a male sings during the laying period to encourage his mate to increase the investment in the brood. The simultaneous performance of nocturnal song and a high level of diurnal singing during egg laying may be costly, and hence could indicate male quality. Therefore, females may adjust their reproductive effort with regard to male singing activity during egg laying (Sheldon 2000). Females might modify the number of eggs (Kroodsma 1976) or adjust the allocation of resources into the yolk (Gil et al. 1999b).

However, female birds begin to deposit yolk 3–5 days before egg laying (King 1973). To encourage their mates efficiently, males should therefore increase their song output some days before the first egg is laid. However, mated males never started nocturnal song more than a day before the first egg was laid.

Alternatively, males could honestly announce the fertility of their own mates to rival males by singing more, to signal their good condition and thus their ability to defend paternity. This 'fertility announcement hypothesis' (Møller 1991) predicts the highest singing effort when the females are most fertile. We found that mated males had their highest diurnal singing activity and also resumed nocturnal singing during the laying period. In his hypothesis, Møller (1991) made no distinction between the prelaying and the laying period, treating both as a time of peak fertility. Similar to our results, Gil et al. (1999a) found a peak of singing activity during the laying and not during the prelaying period in the willow warbler, *Phylloscopus trochilus*. They regarded this as evidence against singing as an announcement of fertility, apparently assuming that females are not fertile during egg laying. Indeed, the receptivity of females for new sperm seems to be lower during egg laying (Brillard & Bakst 1990), and, accordingly, most species show a marked reduction or total cessation of copulation after the first egg is laid (Birkhead & Møller 1992). However, as long as it cannot be excluded that, during egg laying, copulations take place and may lead to a reasonable number of fertilizations, it remains possible that elevated singing activity during this period serves to defend paternity.

Finally, males may sing more during the laying period of their mates to attract females for extrapair copulations (Hasselquist et al. 1996). In this case, it would be interesting to investigate why males appear to resume nocturnal song at the start of their mate's egg laying and not earlier, when neighbouring females might already be fertile.

Several other field studies have found an elevated level of song during egg laying. Of the 13 studies that Gil et al. (1999a) reviewed with regard to the fertility announcement hypothesis, three did not discriminate between the laying period and the prelaying period. Of the remaining 10 studies, at least five reported an elevated level of singing activity or of some other song parameter during egg laying. Therefore, a clear distinction between the prelaying period and the laying period is important for studies that aim to identify the functions of male song during the fertile period of females. More attention should also be paid to the singing of unmated males, because this may increase our understanding of the singing behaviour of their mated conspecifics.

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SEASONAL PATTERNS OF SINGING ACTIVITY VARY WITH TIME OF DAY IN THE NIGHTINGALE (*LUSCINIA MEGARHYNCHOS*)

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Abstract.—Seasonal patterns of singing activity of male birds have been thoroughly studied, but little is known about how those patterns vary with time of day. Here, we censused mated and unmated male Nightingales (*Luscinia megarhynchos*) at four different hours of the day throughout the breeding cycle. In unmated males, singing activity increased until the young hatched in their neighborhood, and the seasonal variation was similar at each of the four hours of the day. In mated males, however, the seasonal patterns of singing activity differed between hours of the day. In morning (about the hour of egg-laying) and during the dusk chorus, the singing activity of mated males was strongly influenced by the females' reproductive state: singing activity was low before egg-laying and during incubation, but high during the egg-laying period. In the dawn chorus, however, singing activity showed a similar seasonal pattern in mated and unmated males and was high until late stages of the breeding cycle. Our results suggest that the social context influences singing behavior to a varying degree across the season, and that this variation also depends on time of day. The hour of data collection thus is an important but often neglected factor when seasonal changes of singing activity are studied. *Received 17 October 2002, accepted 15 September 2003.*

Résumé.—L'évolution saisonnière du chant chez les oiseaux mâles a été largement étudiée, mais peu de choses sont connues quant à sa variation au cours de la journée. Dans cette étude, nous avons recensé des mâles de *Luscinia megarhynchos* accouplés ou non, à quatre différentes heures de la journée tout au long du cycle de reproduction. Pour les mâles non accouplés, les activités de chants augmentaient jusqu'à l'éclosion des jeunes dans le voisinage, et la variation saisonnière était similaire pour les quatre différentes heures de la journée. Par contre, pour les mâles accouplés, les profils saisonniers du chant différaient entre les heures de la journée. Le matin (à l'heure de ponte) et au crépuscule, les chants des mâles accouplés étaient fortement influencés par le stade de reproduction des femelles. En effet, les chants étaient peu fréquents avant la ponte et au cours de l'incubation, mais ils étaient plus fréquents durant la période de ponte. Néanmoins, à l'aube, les chants montraient un profil saisonnier similaire pour les mâles, qu'ils soient accouplés ou non, et demeuraient très fréquents jusqu'aux dernières phases du cycle de reproduction. Nos résultats suggèrent que le contexte social influence le comportement de chant de manière plus ou moins importante au cours de la saison, et que cette variation dépend également du moment de la journée. La prise en considération de la chronologie journalière est un facteur d'importance souvent négligé dans les études portant sur l'évolution saisonnière du chant.

A primary step in identifying the functions of a particular bird species' song is to examine the relationship between time of day or season and amount of singing (Hutchinson et al. 1993, Catchpole and Slater 1995). Numerous studies have correlated singing activity with the periods of the females' breeding cycle (reviewed in Møller 1991 and Gil et al. 1999). In recent years, much attention has been focused on male song when females are fertile. An elevated singing activity during that period is commonly interpreted to function in sperm competition (Møller 1991), to attract additional social mates (Hasselquist and Bensch 1991), or to stimulate or encourage the mate (Pinxten and Eens 1998, Amrhein et al. 2002). Several authors did not find a peak of song during the fertile period (Pärt 1991, Gil et al. 1999) and questioned in particular the sperm competition hypothesis. However, the results of the different studies are difficult to compare, because the time of

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day that data were collected varied between studies. Some authors investigated seasonally changing singing activity at dawn (Cuthill and Macdonald 1990, Pärt 1991, Welling et al. 1995, Rodrigues 1996), but in most studies data were collected throughout the morning (Johnson and Kermott 1991, Hanski and Laurila 1993, Eens et al. 1994, Merilä and Sorjonen 1994, Krokene et al. 1996, Nemeth 1996, Gil et al. 1999, Forstmeier and Balsby 2002). Other studies covered almost all hours of daylight (Sheldon 1994, Currie et al. 1998, Amrhein et al. 2002).

Pinxten and Eens (1998) investigated singing activity during the fertile period in European Starlings (*Sturnus vulgaris*) and found that males sang more in late morning, following egg-laying, than in early morning. They assumed that the hour after egg-laying is a time of peak fertility (but see Birkhead et al. 1996) and suggested that the elevated singing activity serves to protect paternity. We expect that in such a species a diel peak of song in the late morning is restricted to the period of the breeding cycle when females lay eggs. Furthermore, a seasonal peak of song during the fertile period should be found mainly if singing activity is censused at a time of day when egg-laying takes place. In contrast, the seasonal pattern of singing at other times of the day may be less influenced by the reproductive state of females and therefore reveal no clear peak during the fertile period. That would mean that diel patterns can influence the results of studies examining seasonal singing patterns.

However, little is known about how diel patterns in male song relate to changes in female reproductive state (Staicer et al. 1996). Day-round activity data for individual breeding pairs are difficult to obtain for all periods of the breeding cycle, because individuals do not breed perfectly synchronously and therefore almost daily data collection is required. Until now, studies that investigated day-round singing patterns in the course of seasons made population-wide surveys without reference to the breeding cycles of individual females (Catchpole 1973, Sorjonen 1977, Merilä and Sorjonen 1994, Kloubec and Capek 2000).

Here, we used a new approach by sampling male Nightingales (*Luscinia megarhynchos*) four times every day throughout the breeding cycle. We examined seasonal changes of singing activity at dawn, in the morning at a time of day when egg-laying takes place, in the afternoon, and at dusk. Our aim was to determine if the seasonal patterns of singing activity vary with time of day. We also investigated how seasonal patterns differed between mated males and males that remained unmated. We hypothesized that at those times of the day, when the reproductive state of females most strongly influences the singing activity of their mates, seasonal changes in singing activity should most strongly differ between mated males and males that remained unmated.

METHODS

General methods.—The study was conducted from April to June 2002 and 2003 at the Petite Camargue Alsacienne in France, 10 km north of Basel, Switzerland. The first males were observed on 12 April 2002 and 13 April 2003, respectively, and the first females were observed on 20 April in both years. All male and female subjects were color-banded. For the first clutches of 13 females, egg-laying dates were determined by direct observation during the laying period (n = 6) or were calculated from hatching date (n = 2) and the age of the nestlings (n = 5). Clutch sizes were four (n = 2), five (n = 10), and six (n = 1). For all mates of the 13 females, we have a complete data set on singing activity for the first four periods of the breeding cycle (see below). For the last two periods, the sample size was reduced to 10 and 6 mated males, respectively, because 6 broods were depredated and 1 male was found dead on a road (apparently struck by a car). Values from all periods are depicted in graphs, whereas statistical analyses include only the complete data set from the first four periods. In addition to the 13 pairs, 13 unpaired territorial males were monitored for which the term "bachelors" was used to avoid confusion with the unpaired period of all males before arrival of the females. In all bachelor territories, we monitored for the presence of a female by regularly mist-netting throughout the season. Bachelors were immediate territorial neighbors of the mated subjects (n = 7) or were separated from a mated subject by up to three other territories (n = 6). For bachelors, the season was subdivided according to the breeding periods of their immediate mated neighbors or, for more separated bachelor territories, according to the mean breeding dates of the 13 females. The sample size for bachelors is 13 for all periods, except the last period, in which three birds deserted their territories. Most subjects were older than one year; two mated males and two bachelors were yearlings (i.e. birds that fledged in the previous year), and one bachelor was of undetermined age.

Periods of the breeding cycle.—The periods of the breeding cycle were defined as follows: the unpaired period was from the day a male started to advertise a territory until the day before a female settled in his territory (4–14 days, $\bar{x}$ ± SD = 8 ± 3, $n = 13$). The pre-laying period was from the day a female settled until the day before the first egg was laid (5–13 days, $\bar{x}$ ± SD = 8 ± 3, $n = 13$). The laying period was from the day the first egg was laid to the day the last egg was laid (five days in most cases). The incubation period was from the day after the last egg was laid until the day before the young hatched (12 days as determined by the observation of $n = 6$ broods). The nestling period was from the day the young hatched to the day before they left the nest (10, 11, or 12 days; each $n = 2$). The fledgling period was from the day the young left the nest until we finished our field work (4–12 days, $\bar{x}$ ± SD = 9 ± 3, $n = 6$), and young are fed for 14 to 20 days after leaving the nest (Cramp 1988).

Singing activity.—Four rounds were made on the study site each day from 15 April to 9 June 2002 (56 days) and from 15 April to 7 June 2003 (54 days). Singing activity of a male is expressed as the proportion of rounds per period or per day on which it was heard singing. This measure of singing activity has been shown to be a sensitive tool in an earlier study (Amrhein et al. 2002). During each round, we passed by a male's territory for 30 s. This duration was sufficient to determine whether the bird was singing, because during a song bout, males sing continuously with pauses of about 3 to 5 s between songs. The direction of the rounds was changed from day to day, and the duration of each round was 1 h. The dawn round started 1.25 h before sunrise. The dusk round started at sunset. The morning round started at 0900 hours (CEST); this time was chosen because egg-laying is between 0800 and 1100 hours in Nightingales (Amrhein et al. 2002). The afternoon round started at 1400 hours, to include a time with relatively low singing activity. To survey nocturnal singing behavior, an additional round was made starting at midnight (this round was not included in the analyses of singing activity).

Statistics.—All sample sizes refer to the number of individuals; none of the subjects sampled in 2002 were also sampled in 2003. The proportional data were normalized by applying an Anscombe transformation (Zar 1996). The general linear model (GLM) repeated measures procedures (SPSS V.11) were used, with time of day and periods of the breeding cycle as within-subjects factors (four levels each) and mating status as between-subjects factor.

RESULTS

Mated males sang most during the laying period and sang least during the period of feeding nestlings, whereas the singing activity of bachelors continuously increased until the end of the incubation period (Fig. 1). After arrival of a female, singing activity in mated males decreased until shortly before egg-laying, then increased at the day the first egg was laid and remained high until the first days of incubation (Fig. 2).

For the following statistical analyses, we consider only the complete data set from the first

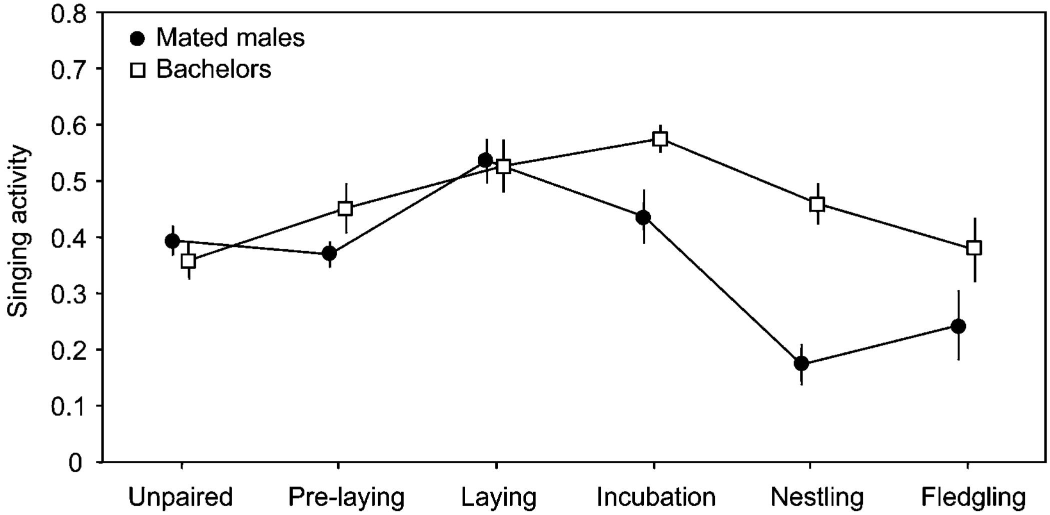

Fig. 1. Mean (± SE) singing activity of male Nightingales over six periods of the breeding cycle, based on four rounds conducted on the study site each day. Singing activity of a male is expressed as the proportion of rounds per period on which it was heard singing. For bachelors ($n = 13$; fledgling period: $n = 10$), the season was subdivided according to the breeding periods of the mated males ($n = 13$; nestling period: $n = 10$; fledgling period: $n = 6$).

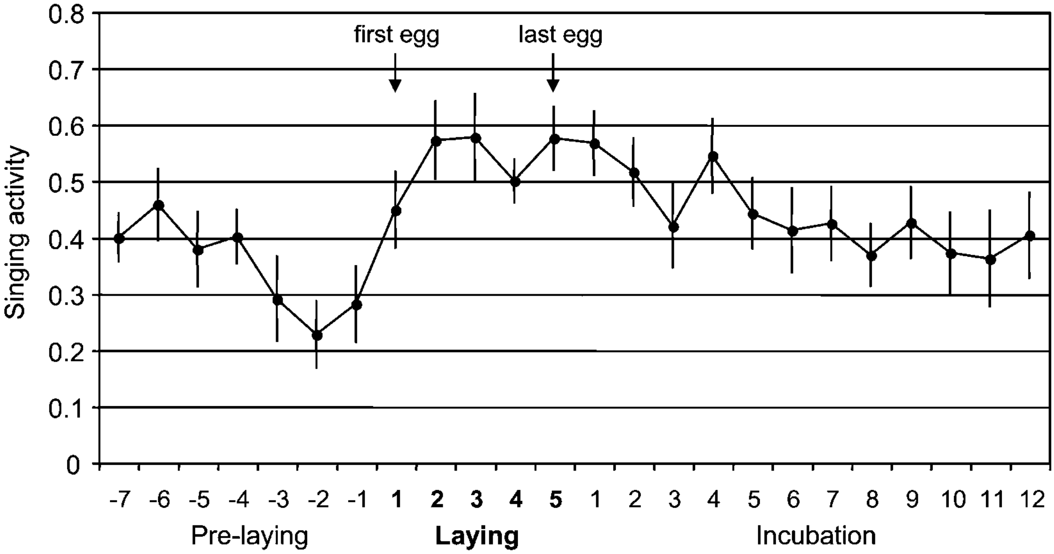

Fig. 2. Mean (± SE) singing activity per day in mated male Nightingales over three periods of the breeding cycle. Singing activity of a male is expressed as the proportion of four rounds per day on which it was heard singing. The last females settled in a male's territory on day –5, so the sample size is $n = 13$ for every day except for day –6 ($n = 11$) and day –7 ($n = 9$).

four periods of the breeding cycle (unpaired period until incubation period). The overall diurnal song output differed between periods of the breeding cycle (Fig. 3; $F = 11.29$, df = 3 and 72, $P < 0.001$), but not between mated males and bachelors ($F = 1.76$, df = 1 and 24, $P = 0.19$). The overall song output differed also between hours of the day ($F = 125.55$, df = 3 and 72, $P < 0.001$), with the highest singing activity at dawn and the lowest singing activity in the afternoon (in both mated males and bachelors; Fig. 3). To examine the interaction between seasonal and diurnal changes of singing activity, we made two separate analyses. In mated males, the interaction between periods of the breeding cycle and time of day was significant ($F = 3.75$, df = 9 and 108, $P < 0.001$), which suggests that the seasonal patterns of singing activity vary with time of day (Fig. 3A). In bachelors, the same interaction was not significant ($F = 1.61$, df = 9 and 108, $P = 0.12$), reflecting the finding that the seasonal patterns of singing activity were similar at different hours of the day (Fig. 3B).

To examine further how the seasonal patterns varied according to mating status, we made a separate analysis for each time of day.

Dawn.—At dawn, differences in singing activity between periods of the breeding cycle were significant ($F = 4.61$, df = 3 and 72, $P = 0.005$), and bachelors sang more than mated males (Fig. 3; $F = 7.09$, df = 1 and 24, $P = 0.014$). However, the interaction between mating status and periods of the breeding cycle was not significant ($F = 1.85$, df = 3 and 72, $P = 0.15$), reflecting the finding that the patterns of seasonally changing singing activity were similar in mated males and bachelors. In both mated and unmated males, elevated singing activity at dawn was maintained until the end of the nestling period (Fig. 3).

Morning.—At 0900 hours, singing activity differed between periods of the breeding cycle ($F = 7.61$, df = 3 and 72, $P < 0.001$), but not between mated males and bachelors ($F = 2.93$, df = 1 and 24, $P = 0.10$). However, the interaction between mating status and breeding cycle was significant ($F = 9.93$, df = 3 and 72, $P < 0.001$), which suggests that at this time of the day there are different patterns of seasonally changing singing activity in mated males and bachelors. In mated males, this pattern was characterized by low singing activity in the pre-laying and incubation periods, and by a peak of singing activity when the females were laying eggs (Fig. 3A).

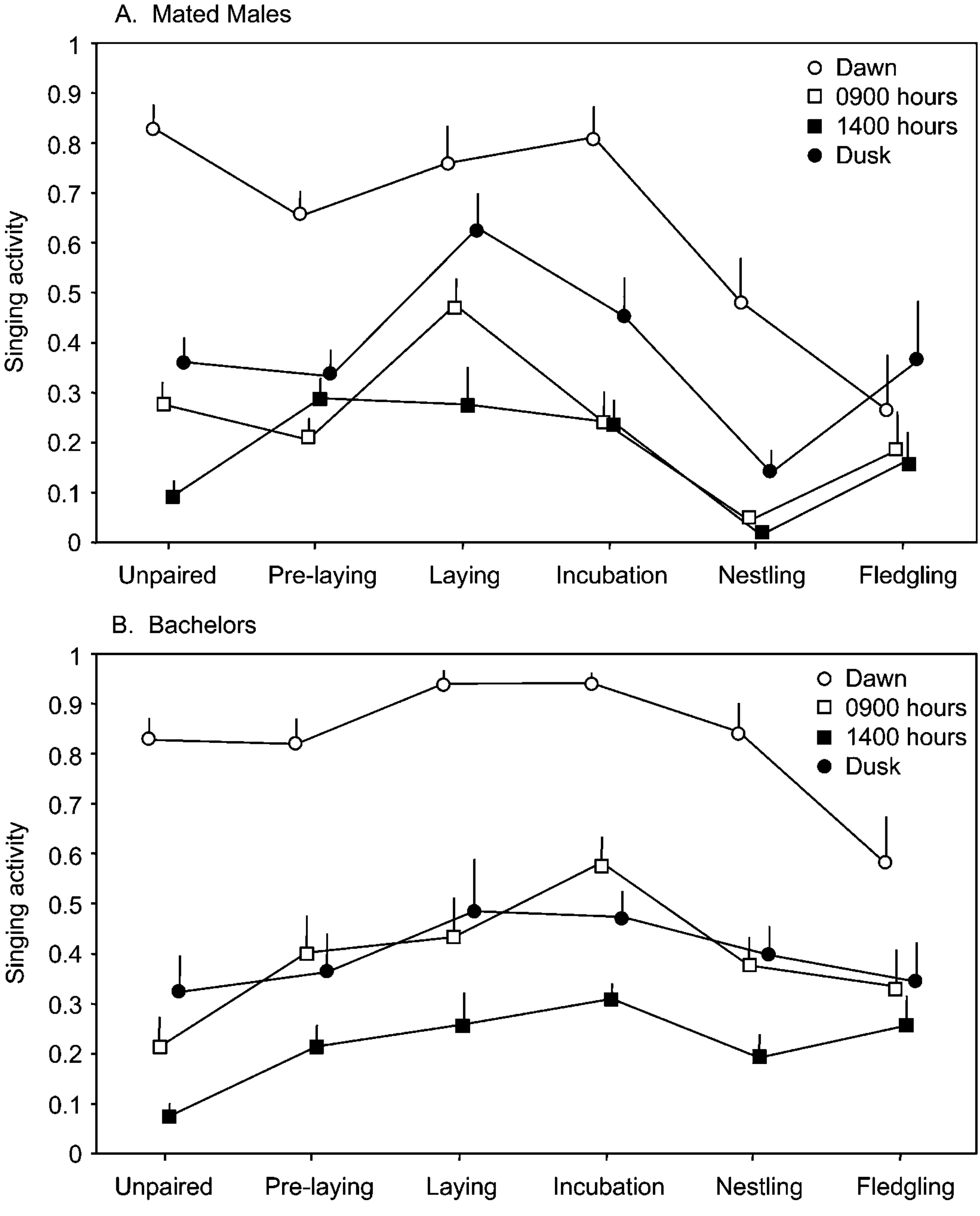

Fig. 3. Mean (+ SE) singing activity of mated male Nightingales (A) and of bachelors (B) at four different hours of the day. For the definition of singing activity and sample sizes, see Figure 1.

Afternoon.—At 1400 hours, singing activity differed between periods of the breeding cycle ($F = 7.5$, df = 3 and 72, $P < 0.001$), but not between mated males and bachelors ($F = 0.02$, df = 1 and 24, $P = 0.89$). Also, the seasonal changes in singing activity were not found to differ between mated males and bachelors (interaction: $F = 1.01$, df = 3 and 72, $P = 0.39$).

Dusk.—At dusk, singing activity differed between periods of the breeding cycle ($F = 6.09$, df = 3 and 72, $P < 0.001$), but not between mated males and bachelors ($F = 0.19$, df = 1 and 24, $P = 0.66$). Similar to the pattern at 0900 hours, there was a peak of singing activity in mated males during the egg-laying period (Fig. 3A). However, the interaction between mating status and breeding cycle was not significant at dusk ($F = 0.78$, df = 3 and 72, $P = 0.51$).

Nocturnal song.—Mated males sang nocturnal song before pairing and partly during the egg-laying and incubation period; bachelors sang nocturnal song throughout the season. Of 13 mated males, 1 male was never heard singing at night. Twelve mated males sang nocturnal song during a total of 5 to 27 nights ($\bar{x} \pm \text{SD} = 11 \pm 7$). Of those 12 males, 11 males sang before pairing during 2 to 14 nights ($\bar{x} \pm \text{SD} = 8 \pm 3$). All males stopped nocturnal song upon pairing, but one mated male stopped singing for only two nights and then continued to sing until the fourth day of the incubation period. Additionally, six mated males resumed nocturnal song during the egg-laying period for two to six nights ($\bar{x} \pm \text{SD} = 4 \pm 1$), starting in the night before the first egg was laid, or one or two nights later (each $n = 2$). Of those six males, four males continued to sing during the incubation period for two to seven nights ($\bar{x} \pm \text{SD} = 4 \pm 2$). One mated male resumed nocturnal song during the nestling period after its mate had left the territory following depredation of the brood. All 13 bachelors sang nocturnal song throughout the season for a period of 31 to 48 days ($\bar{x} \pm \text{SD} = 40 \pm 5$).

Discussion

Male Nightingales sang most at dawn and sang least in the afternoon, whereas they sang at an intermediate level in the morning and at dusk. In unmated males, that pattern was consistent throughout the breeding season. In mated males, however, the diel patterns of singing activity varied between periods of the breeding cycle.

The difference in singing patterns between mated and unmated males suggests that singing activity in mated males was influenced by the reproductive state of the females. That influence on singing activity was strong in the morning and at dusk. In contrast, the singing activity of mated males at dawn and in the afternoon appeared to be less influenced by the reproductive state of females. Although mated males sang less at dawn than bachelors, they still maintained high singing activity at dawn until the end of the nestling period. Those results are in line with studies on the Collared Flycatcher (*Ficedula albicollis*; Pärt 1991), on the Chiffchaff (*Phylloscopus collybita*; Rodrigues 1996), and on wood-warblers (Staicer et al. 1996). In those species, singing activity at dawn remained high until late stages of the breeding cycle or was not affected by mating status. Such findings support the idea that singing during the dawn chorus is important to defend the territory against rival males or to adjust social relationships among territorial neighbors (Staicer et al. 1996). If dawn singing would mainly serve to attract a mate, it should be confined to unmated males; if dawn singing would mainly serve to guard or stimulate a fertile mate, it should peak during the pre-laying or laying period in mated males.

In the morning, about the hour of egg-laying, mated males showed low singing activity in the pre-laying and incubation periods but showed high singing activity when the females actually were laying eggs. At that time of day, the seasonal pattern was significantly different in bachelors, which continuously increased their singing activity until the end of the incubation period. Also at dusk, the singing activity of mated males was elevated during the laying period in comparison to the pre-laying and incubation periods. It appears that in mated males the patterns in the morning and at dusk are largely responsible for the overall peak of singing activity during the laying period and during the first days of incubation. For the same time period, half of the mated males also resumed nocturnal singing that they had stopped after pairing, which confirms our previous findings (Amrhein et al. 2002). The elevated singing activity during the laying period could serve to encourage the female to increase the investment in the brood according to male quality (Sheldon 2000, Amrhein et al. 2002). Furthermore, high singing activity during egg-laying may serve to protect paternity, either through repelling rival males or through stimulating the female to solicit copulations (Pinxten and Eens 1998). However, as Birkhead et al. (1996) have pointed out, copulations around the hour of egg-laying are not very likely to result in fertilization, making it rarely worthwhile for pair members to copulate or for males to guard the female in the morning during the laying period. Alternatively, mated males may sing more during egg-laying because in the pre-laying and incubation periods they are engaged in other activities that conflict with singing. If in Nightingales, as in many other bird species, pair members stop copulating once egg-laying has started (Birkhead and Møller 1993), the male may be less closely associated to the female during egg-laying then before and thus have more time to sing. It should be possible to address these functional issues by investigating how males sing depending on the proximity to the female. In the present study, the day-by-day analysis showed that singing activity of mated males was particularly low during the three days before the first egg was laid. If we assume that this time period is when females reach peak fertility, our results may add to the evidence that singing activity is not important as a paternity guard (Sheldon 1994, Gil et al. 1999).

Our study shows that seasonal patterns of singing activity can differ between hours of the day. In mated male Nightingales, we found high singing activity at dawn until late stages of the breeding cycle; but in the morning and at dusk, the singing activity was elevated only when females were laying eggs. To address the functions of those singing patterns, subsequent studies are needed that investigate to whom song is directed at which time of season and day. Nevertheless, it appears that the social context influences singing behavior to a varying degree across the season, and that this variation also depends on time of day. The hour of data collection thus is an important factor when seasonal changes of singing activity are studied.

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III

THE ROYAL SOCIETY
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Non-territorial nightingales prospect territories during the dawn chorus

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Male songbirds usually sing when they have occupied a territory, but the territory prospecting of non-territorial males is more elusive and has been rarely studied. Here, we simulated newly arriving, non-territorial males by translocating unmated male nightingales (*Luscinia megarhynchos*) to our study site. We show that territory prospecting of translocated males was largely confined to the hour before sunrise. The radio-tagged males made extensive excursions visiting several singing males at dawn, but after dawn they remained stationary outside occupied territories. As in many other songbird species, dawn was also the time when resident males sang the most. These results suggest that non-territorial male nightingales use the dawn chorus to assess singing residents or territory occupancy. For resident males, dawn singing may be important to announce territory occupancy to prospecting males and may thus play a role in territory maintenance.

Keywords: dawn chorus; non-territorial males; floaters; radio tracking; *Luscinia megarhynchos*

1. INTRODUCTION

The hour before sunrise is a time of peak singing activity in the males of many bird species (Staicer *et al.* 1996). Intensified singing during this dawn chorus has been hypothesized as serving to attract a mate (McNamara *et al.* 1987), to guard a fertile female (Mace 1987; Welling *et al.* 1995) or to defend the territory against rival males (Kacelnik & Krebs 1983). Given that birds must, for any of those reasons, spend some part of the day singing, dynamic modelling has further demonstrated that environmental factors could generate a dawn peak of singing (McNamara *et al.* 1987; Hutchinson *et al.* 1993; Hutchinson 2002). Reviewing the hypotheses on the dawn chorus, Staicer *et al.* (1996) have pointed out that mate attraction or mate guarding cannot explain why, in many bird species, dawn singing extends well beyond the fertile period of females or is unaffected by male mating status. For example, in the socially monogamous nightingale (*Luscinia megarhynchos*), both mated and unmated males show high singing activity at dawn until late stages of the breeding cycle (Amrhein *et al.* 2004). Such singing patterns are consistent with the hypothesis that song serves to defend the territory against rival males. Krebs (1977) demonstrated, by removing males and replacing them with loudspeakers, that broadcasting song delays reoccupation of territories in the great tit (*Parus major*). Krebs suggested that song has a role in territory maintenance and that non-territorial males use song to assess the occupancy of an area. Kacelnik & Krebs (1983) then argued that, if territory prospecting by non-territorial birds peaks at dawn, this could reinforce the need to sing at dawn for resident males. In their study on the great tit, however, Kacelnik & Krebs (1983) present data on invasions by potential settlers only for the hours after dawn.

In several bird species, non-territorial individuals are common. They are generally referred to as ‘floaters’ and have been shown to visit breeding territories regularly (Smith 1978; Zack & Stutchbury 1992). Also in highly territorial species, there are often many non-breeding males (Ligon 1999). Non-breeding males may defend a territory, but after a certain time desert it to settle somewhere else. Newly arriving, territory prospecting males may be another territorial threat to residents. It is, however, difficult to observe non-breeding or newly arriving males in the short time period when they actually search for a place to settle. One way to investigate the spatial behaviour of such floaters is to translocate birds from one area to another. This procedure serves to control for the subjects’ settlement status and to exclude familiarity with local territories. To date, translocations have been used to investigate female mate sampling behaviour (Dale *et al.* 1990; Bensch & Hasselquist 1992). Here, we applied the same method to study male territory sampling behaviour. We observed translocated radio-tagged nightingales throughout the day and found that they prospected territories almost exclusively at dawn, when resident males had their peak of singing activity.

2. MATERIAL AND METHODS

(a) *General*

The translocated males were released during the breeding season of 2002 at the Petite Camargue Alsacienne in the Upper Rhine Valley in France, where we had surveyed about 50 nightingale territories per year since 1994 (Amrhein *et al.* 2002). The capture site was 70 km to the north of the release site. At both sites, we monitored territories and mating status of all males throughout the breeding season. We ascertained the males’ mating status by observing their nocturnal singing behaviour, because it is only unmated males who sing regularly at night for a prolonged period (Amrhein *et al.* 2002, 2004). At the release site, we controlled the identity of males and the presence of females or floaters by regularly mist-netting throughout the season; the first males arrived on 12 April, and the females settled between 20 April and 8 May.

(b) *Translocation*

From 16 April to 2 June 2002, we translocated 13 male nightingales at intervals of 4 ± 2 days (mean ± s.d.) between translocations of a male. For translocations, we captured unmated males and glued radio-transmitters to their back feathers. We released the birds at about 10.00, within 4 hours of capture, and tracked all translocated males continuously during their first 2 days at the release site. We used telemetry equipment by Titley Electronics, Australia: three element Yagi antennae, Regal 2000 receivers and LT1 transmitters (equipment mass of 0.9 g = 4.1% of the average mass of our subjects).

(c) *Singing activity of resident males*

From 15 April to 9 June 2002, we made five rounds of inspection at the release site each day. Singing activity of a male is expressed as the proportion of rounds on which it was heard singing (Amrhein *et al.* 2002, 2004). Rounds followed a fixed route of 4500 m; we changed the direction of the rounds from day to day, and the duration of each round was 1 hour. The dawn round started 1.25 hours before sunrise. The morning round started at 09.00 (CEST). The afternoon round started at 14.00, the dusk round at sunset and the nocturnal round at midnight. For statistical analysis, we normalized the proportional data by applying an Anscombe transformation (Zar 1996).

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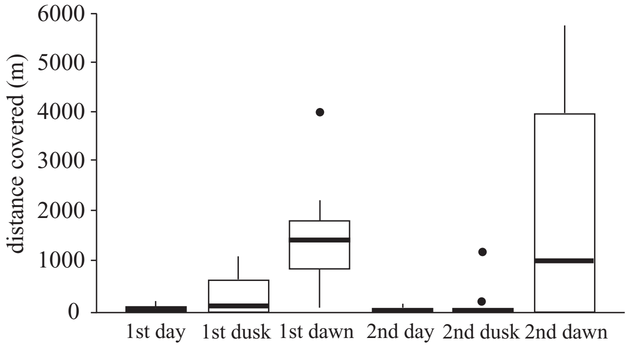

Figure 1. Diel pattern of movements of non-territorial male nightingales. For their first 2 days after translocation to the study site, movements of 13 radio-tagged males are given as the number of metres covered per hour (second dawn: $n = 9$). Boxes are median and 25th and 75th percentiles, whiskers are non-outlier ranges and dots are outliers. The first day is from releasing time at about 10.00 until before dusk. The lengths of the movements varied depending on time of day (Friedman test, $n = 9$, d.f. = 5, $p = 0.002$), with a burst of movement during the dawn chorus in the hour before sunrise.

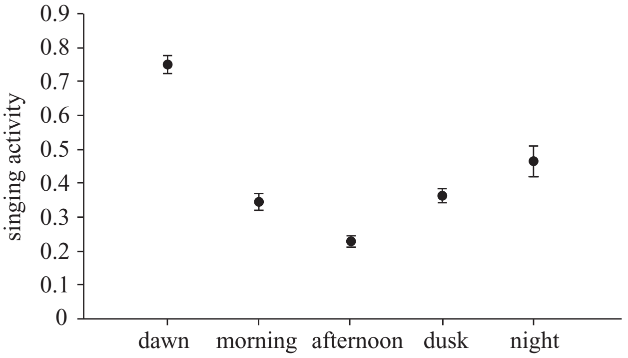

Figure 2. Mean (± s.e.) singing activity of 43 resident male nightingales, based on five rounds conducted on the study site each day throughout the breeding season. Singing activity of a male is expressed as the proportion of rounds on which it was heard singing. The probability of encountering a male nightingale singing was highest at dawn (repeated-measures ANOVA, $F_{4,168} = 53.67$, $p < 0.001$).

3. RESULTS

(a) *Translocation*

During the day, the translocated males remained almost stationary (figure 1). In the first dusk after translocation, seven out of the 13 males made short excursions with a length of 650 ± 410 m (mean ± s.d.) and a duration of 20 ± 4 min, starting 9 ± 5 min after sunset. No movements were observed during the night. It was only at dawn that most males made significant movements (figure 1). During the first dawn, two translocated males moved 30 and 120 m, respectively, and spent most of the time singing outside the territories of resident males. Eleven translocated males that only exceptionally sang covered 1700 ± 900 m in 54 ± 25 min and stopped moving 15 ± 11 min before sunrise. The lengths of dawn trips did not change as the season progressed (linear regression, $F_{1,11} = 0.04$, $p = 0.84$). During the first dawn trip, the 11 males visited 5 ± 3 occupied territories, often sitting close to the singing resident, and spent more time stationary inside occupied territories (25 ± 15 min) than outside (14 ± 9 min; Wilcoxon signed ranks test, $Z = -1.96$, $n = 11$, $p = 0.05$). Eight translocated males that visited both mated and unmated residents spent more time per visit in territories where a female was present (6.8 ± 1.9 min) than in territories of unmated males (3.8 ± 1.8 min; Wilcoxon signed ranks test, $Z = -2.1$, $n = 8$, $p = 0.04$). After dawn, males spent more daylight hours outside than inside occupied territories (Wilcoxon signed ranks test, $Z = -2.17$, $n = 13$, $p = 0.03$). During the second dawn we followed nine males, six of which again made excursions with a length of 3100 ± 2340 m. Eleven translocated males left the release site after 2–5 days and returned to the site of capture; two males settled in unoccupied territories that they had visited during a dawn or dusk trip.

(b) *Behaviour of resident males*

We monitored the singing activity of 43 resident males. The probability of encountering a resident nightingale singing was highest at dawn and lowest in the afternoon (figure 2). Out of 43 resident males, 21 males (49%) remained unmated and sang regularly at night in addition to diurnal song. All unmated males were territorial for some part of the breeding season. However, 11 unmated males left their territories after 6–46 days (33 ± 12 days) and were observed in other parts of the study site. One of those floating males was radio-tagged and showed similar behaviour to the translocated males. On 23 May, it sang at dawn in a previously unoccupied territory until 24 min before sunrise, when it moved 600 m to the border of an occupied territory and stayed stationary for the rest of the day.

4. DISCUSSION

We found that translocated male nightingales moved around extensively at dawn, rather than at other times of the day or night. During those dawn movements, the translocated males visited several resident males, but after dawn they remained stationary outside occupied territories. Dawn was also the time that resident males sang most.

Our study was intended to simulate non-territorial, newly arriving males that prospect an unfamiliar area. Although the translocation procedure may have influenced the birds in many ways, we do not expect that the dawn peak of activity can be attributed solely to adverse effects of the handling. Furthermore, a resident, not translocated floater showed similar behaviour. Yet we do not know when the translocated birds decided whether to stay at the release site or to return to the capture site; both the males that returned and the males that stayed may have prospected the area on the search either for a territory or simply for a place to rest. Whichever is the case, however, their territory prospecting behaviour remains interesting. During their dawn trips, the translocated birds apparently were attracted by singing residents, since they intruded territories and approached the singing males. These intrusions may have served to assess singing males or territory quality; the presence of a female could also have been of interest, since translocated males spent more time in territories of mated than of unmated males.

Most striking, however, is that territory prospecting was largely confined to the hour when resident males sang the most. The causes and implications of this correlation remain speculative at present. It may well be that both singing and territory prospecting had their peaks at dawn owing to environmental factors that favour these behaviours above foraging (Hutchinson 2002). However, the coincidence of the behaviours could also be of some adaptive value. Dawn seems to be the best hour for territory prospecting, since this time was when most residents sang. By contrast, the probability of encountering a resident male announcing its territory was lower at other times of the day and was biased at night when only unmated males regularly sing (Amrhein *et al.* 2002). Non-territorial males may therefore use the dawn chorus to assess singing residents or territory occupancy. For resident males, dawn singing may be important to drive non-territorial males into unoccupied areas and thus to maintain the territory. At the release site, several unmated residents left their territories and moved around after being territorial for a certain time. This could explain why territorial nightingales sing at dawn throughout the breeding season (Amrhein *et al.* 2004). There is evidence for a general territory maintenance function of song in the thrush nightingale (*Luscinia luscinia*), a close relative of the nightingale: Göransson *et al.* (1974) showed that, after removal of resident males, day-round broadcasting of song delays reoccupation of territories.

We suggest two ways to explore further the territory maintenance hypothesis of dawn singing. First, speaker replacement experiments could test whether song broadcast at dawn delays reoccupation of a territory for longer than song broadcast at other times of the day (Staicer *et al.* 1996). Second, the territory prospecting behaviour of non-territorial males could be incorporated in dynamic programming models of singing and foraging behaviour. The observation that non-territorial males were attracted by dawn singing suggests that resident males should reduce their dawn singing when their females reach peak fertility. Indeed, some studies showed that dawn singing has a shorter duration or a lower volume during the fertile period than afterwards (Pärt 1991; Rodrigues 1996), and mated nightingales reduce their dawn singing activity during the period before egg-laying commences (Amrhein *et al.* 2004). Outside the fertile period, however, singing for territory maintenance and territory prospecting may be shown to be mutually enhancing and thereby to stabilize the pattern that territorial males have a peak of song at dawn.

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IV

Sperm competition or sex ratio: Possible factors influencing singing and spatial behaviour in the nightingale

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Abstract

Extrapair copulations can increase the variation in male reproductive success, and the resulting sperm competition has been shown to be an important component of sexual selection in many species. Here, we show that in the nightingale (*Luscinia megarhynchos*), sperm competition is not likely to be the main factor influencing spatial behaviour and singing activity of males. The rate of extrapair fertilization (7.5% of the offspring) was low as compared to related species, and we found no distinct paternity insurance and extrapair behaviour. Males did not closely guard their females nor did they sing at elevated levels during the days before egg-laying, when females are thought to be most fertile. Pair members were close to each other to varying but, on average, low degrees before egg-laying and showed great intrapair distances once egg-laying had started. Females were not found to visit other territories, and males made extra-territorial excursions only after egg-laying had begun, to visit mostly territories in which the females were incubating. We argue that possible extrapair behaviour is under female control in the nightingale, and that male extra-territorial excursions mainly serve to gather information on territory occupancy by males and females or to explore social relationships among neighbours. Such information may be vital for defending the own territory in the current season and to succeed in competition for territories and social mates in subsequent breeding seasons. In seven years of study, the average proportion of unpaired males was 33%, and the operational sex ratio (the number of males per females that are ready to mate) remained male-biased throughout the breeding season. We suggest that these sex ratios lead to a greater variation in reproductive success and cause more competition among males than we would expect to result from the rate of cuckoldry.

Introduction

In many bird species, there is considerable variation among males in reproductive success due to sperm competition, some males achieving extrapair paternity and some males loosing paternity in the own brood (Birkhead 1998; Møller & Ninni 1998). Accordingly, it is thought that sexual selection has favoured behavioural traits that ensure paternity and increase the chance of obtaining extrapair copulations. Among the possible paternity defence strategies, the importance of close mate guarding and the function of territorial song as a keep-out signal to cuckolder males is much debated. For some species, it has been shown that mate guarding can diminish paternity loss (Birkhead 1998; Komdeur et al. 1999; Chuang-Dobbs et al. 2001). Furthermore, studies which found low intensity of mate guarding at low levels of extrapair paternity indirectly support the view that mate guarding behaviour is connected with cuckoldry (Chek et al. 1996; Schleicher et al. 1997). In other species, however, elevated levels of extrapair paternity occur in spite of high mate guarding activity (Kempenaers et al. 1995; Johnsen et al. 1998) or else are associated with low levels of mate guarding (Chek & Robertson 1994; Fedy et al. 2002). In those cases, it has been argued that females have control over extrapair fertilization and that their males simply do the best of a bad job or give up their mate guarding efforts in favour of other strategies. Low mate guarding activity could be explained by the males relying on paternity guards such as frequent intrapair copulations. Low mate guarding could also result from a trade-off between mate guarding and pursuing extrapair copulations (Westneat et al. 1990; Chuang-Dobbs et al. 2001). For example, male hooded warblers (*Wilsonia citrina*) have been shown to regularly intrude into territories of fertile females, which could increase their chance to obtain extrapair copulations but potentially reduces the time males can spend for mate guarding (Stutchbury 1998). However, in several species, it is the females that control extrapair fertilization and intrude into other territories to solicit copulations (Smith 1988; Kempenaers et al. 1992; Neudorf et al. 1997; Double & Cockburn 2000). In males, not all extra-territorial excursions may lead to extrapair fertilizations or even be related to sperm competition. For example, male chaffinches (*Fringilla coelebs*) have been shown to regularly visit other territories throughout the breeding season but not selectively those of fertile females (Hanski 1992), and to spend a considerable proportion of time foraging outside their song territories and in territories of other males (Maciejok et al. 1995).

In our study population of nightingales (*Luscinia megarhynchos*), up to 49% of the males remain unpaired throughout the breeding season, and unpaired, non-territorial males often move around to prospect occupied territories (Amrhein et al. 2004a). Also territorial males could use extra-territorial excursions not necessarily with an exclusive focus on extrapair copulation, but also to gather information on territory occupancy or social relationships among neighbours (Naguib et al. 2004). Likewise, the peak of singing activity that occurs during egg-laying in species like the nightingale (Amrhein et al. 2002) or the willow warbler (*Phylloscopus trochilus*; Gil et al. 1999) could be related to territory maintenance or intrapair communication, rather than to serve mainly in repelling cuckolder males (Amrhein et al. 2004b).

In the socially monogamous nightingale, a long-term male-biased adult sex ratio would mean that every year some proportion of males fail to obtain social mates. The variation in reproductive success among males that would result from the male-biased sex ratio could be greater than the variation caused by extrapair fertilization. In this case, we would expect the spatial behaviour of male nightingales to be related less to sperm competition and more to mate attraction and the acquisition or maintenance of a territory, which is an essential prerequisite for the attraction of a female and successful breeding (Catchpole & Slater 1995).

One of the first hypotheses on sexual selection in monogamous birds postulated that females arrive on the breeding grounds later than males and cause variation in reproductive success by choosing among the males already present (reviewed in Kirkpatrick et al. 1990). The operational sex ratio, i.e. the number of males per females that are ready to mate, may thus be strongly male-biased especially in the start of the breeding season, thereby providing a third opportunity for sexual selection (Kvarnemo & Ahnesjö 1996).

Here, we used microsatellite genotyping to examine if variation in reproductive success among male nightingales could be caused by differences in fertilization success. We also present long-term data on the adult sex ratio in our study population and show how the operational sex ratio develops within a breeding season. Furthermore, we studied behavioural traits that are usually thought to play a role in sperm competition: we examined extra-territorial behaviour, singing activity, and mate guarding, by simultaneous radio tracking of male and female nightingales in three periods of the breeding cycle.

Methods

Settlement patterns and mating status

In the breeding seasons 1997 – 2003, we made daily rounds of inspection at our study site in the Petite Camargue Alsacienne in France (Amrhein et al. 2002, 2004b). We investigated the same area of about 106 ha each year. Arrival date and mating status of males was determined by observing their singing behaviour (it is only unmated males that sing regularly at night for a prolonged period), by visual observation, and by regular mist netting. Each year, we captured and banded the adult birds in up to 86% of the territories. Female arrival date was determined by visual observation or capturing, and in most cases the settlement of a female was indicated by the male stopping to sing at night (Amrhein et al. 2002, 2004b).

Paternity analysis

In 1998 – 2003, we collected blood samples from offspring and both parents in 4 – 8 territories per year (Table 1). We collected blood (approximately 25 µl) in capillary tubes from the brachial vein and stored the blood in PBS/EDTA with NaN_3. DNA was extracted with the DNeasy Tissue kit (Qiagen). We studied paternity using the microsatellite markers LM3, LM6, LM26 (unpublished markers that were cloned from blood samples from our study population of nightingales *Luscinia megaryhnchos*), HrU6 (Primmer et al. 1995), and Mcyµ4 (Double et al. 1997).

We used 1 µl DNA-solution in a 25 µl PCR volume containing 1 – 2 mM MgCl, 2.5 µl of 10X Thermobuffer (500 mM KCl, 100 mM Tris-HCl (pH 9.0) and 1% Triton X-100), 0.2 mM of each dNTP (Eppendorf), and 1 unit of Promega Taq polymerase.

The forward-primer was labelled with fluorescin (Pharmacia Biotech). PCR was run in a Techne progene thermo-DUX cycler. The annealing temperatures used for amplification were 60°C for LM3 (1 mM $MgCl_2$), 57°C for LM6 (1.5 mM $MgCl_2$), 58°C for LM26 (1.5 mM $MgCl_2$), 55°C for HrU6 (2 mM $MgCl_2$), and 49°C for Mcyµ4 (1.5 mM $MgCl_2$). Reaction cycles run at 94°C for 3 min, then 35 times (94°C for 30 sec, individual annealing temperatures for microsatellite markers for 45 sec, 72°C for 60 sec), then 72°C for 5 min.

The success of the amplification was controlled by electrophoresis on a 1.5 – 2% agarose gel stained with ethidium bromide and visualized under ultraviolet light. Included on each gel were a 100 base-pair (bp) ladder (Genecraft) as a size standard and a negative control without DNA.

Amplified samples were mixed with formamide loading dye (4 µl), denatured for 3 min at 90°C, quenched and loaded to a 6% polyarcylamide gel with 7 M urea in a DNA-Sequencer (Pharmacia Biotech). The running condition was 800 V, 60 mA, 50 W, Laserpower 2 mW at 50°C in 0.84 sec intervals for about 180 min. Allele size information was obtained with fragment manager software comparing sample lengths to given standards (50 – 500 bp in steps of 50 bp).

We calculated paternity exclusion power using the allele frequency module of CERVUS (Marshall et al. 1998). Paternity was excluded if at least one locus showed mismatches between putative father and offspring. For the 5 markers combined, the probability of excluding a randomly chosen nonfather was 0.99.

Extra-territorial forays and mate guarding

From 20 April to 14 May 2003, we radio tracked 10 nightingale pairs during 182 hours in total. Our aim was to track each pair during one morning in each of three periods of the breeding cycle: before egg-laying started, during egg-laying, and during incubation. Out of the 10 couples, however, three couples could not be observed during all three periods, due to depredation of the eggs (one nest) or because we captured both members of a pair only after egg-laying had begun; in repeated measures analyses, the data from these three couples were excluded. In the 10 pairs, the males arrived between 13 – 17 April (mean ± *s.d.* = 14 April ± 1 day), and the females arrived between 19 – 27 April (22 April ± 3 days). The first egg was laid between 30 April and 8 May (2 May ± 2 days). The clutch that was initiated on 8 May (in the territory of male no. 10; see Table 2) was likely to be a replacement clutch, since the female was already present in the territory for an unusually long period of 19 days; this clutch excluded, the first eggs in nine pairs were laid between 30 April and 4 May (1 May ± 1 day), suggesting a high level of breeding synchrony in the population (regular second clutches did not occur). The females laid five (n = 9) or six eggs (n = 1), one egg per day, between 7.30 and 10.00 (n = 9 females observed). Most subjects were older than one year; the male no. 1 (Table 2) and the females of the males no. 4 and 6 were yearlings (i.e. birds that fledged in the previous year).

The birds were captured in mist nets, banded in their territory and released within 15 min of capture. We attached radio transmitters to the birds' backs using harnesses (Rappole & Tipton 1991); transmitter mass was 0.9 g = 4.3% of the average mass of our subjects. Upon capturing of a bird, we waited at least 1 day before we started radio tracking, and after data collection we recaptured the birds and removed the transmitters. The tracking sessions took place between 5 – 1 days before the first egg was laid, on the days of laying of egg number 1 – 5, and during the incubation days 3 – 9 (Table 2; incubation day 1 was defined as the day after the last egg was laid). Each tracking session started 1.5 hours before sunrise and lasted for exactly seven hours until between 11.00 and 12.00. Replacement of observers was done without interrupting the tracking session. Both the male and the female were tracked simultaneously by one observer, and every 2 min the locations were recorded on a 1:2000 map of the study site. It was also recorded whether the male was singing on the instant of the radio location; singing activity of a male is expressed as the proportion of radio fixes that it was heard singing.

Male singing territories were defined by plotting the song locations on the map. Extra-territorial excursions were defined as occasions where a subject left the singing territory and visited other nightingale territories. During the excursions, each entry in an occupied nightingale territory was counted as 1 foray (this applied also if the same territory was repeatedly visited). We continuously tracked the subject that left for an excursion and regularly checked its mate to monitor if it stayed in the own territory.

Mate guarding behaviour is commonly measured as the proportion of time a male is closer than 5 or 10 m to the female (Hanski 1992; Johnsen et al. 1998; Komdeur et al. 1999; Tobias & Seddon 2000). We defined the mates as being close to each other if the map entries indicated a distance of maximal 8 m; this value was chosen because the map entries deviated from the true distances between pair members for maximal 8 m (see below), and therefore the least accurate radio fixes with 8 m intrapair distance could mean that the birds were in fact next to each other. For the analysis of singing activity and intrapair distances, we took all radio fixes into account but excluded the periods during extraterritorial excursions; the final number of radio fixes per nightingale couple were 196 – 209 (203 ± 5; n = 8) for the pre-laying period, 147 – 209 (182 ± 22; n = 9) for the laying period, and 147 – 205 (180 ± 21; n = 9) for the incubation period.

To test the accuracy of radio locations, we mimicked the natural working conditions by hiding a pair of transmitters in the bushes of 11 nightingale territories. The distances between the transmitters ranged from 0 – 47.0 m (14 ± 14.4), as measured in the field to the nearest 0.1 m. The field assistants had 2 min to locate the transmitters from outside the bushes, walking the same paths they used during the telemetry sessions. The distances we deduced from their entries in the maps deviated from the true distances between 0 – 8.0 m. In absolute values, the mean deviations over 11 trials of the three field assistants were 2.9 ± 2.5 m, 4.0 ± 3.2 m and 4.1 ± 2.3 m, respectively. When we averaged the deviations per territory, there was a tendency to overestimate short distances and to underestimate larger distances (linear regression, $r^2 = 0.33$, $F_{1,9} = 4.49$, $p = 0.06$).

Telemetry equipment and statistics

We used telemetry equipment by Titley Electronics, Australia: Three element Yagi antennae, Regal 2000 receivers, and LT1 transmitters. All statistical tests are two tailed; descriptive statistics in the text are given as ranges and mean ± *s.d.*. For parametric tests, we normalized the proportional data by applying an Anscombe transformation (Zar 1996).

Results

Extrapair paternity and adult sex ratio

We examined the parentage for 147 offspring in 39 broods from 30 different females, 31 different males and 36 different male-female combinations. We detected extrapair offspring in 9 (23.1%) of the 39 nests, and we found one or two extrapair young per nest (in 7 nests and 2 nests, respectively). Out of 147 young, 11 young (7.5%) were sired by extrapair males. The distribution of extrapair young among broods and among years is given in Table 1. We did not detect offspring with genotypes incompatible to their mother and concluded that there was no intraspecific brood parasitism in our sample. Out of the 39 broods, 8 were replacement clutches that were initiated after the first clutches were depredated or inundated. In those replacement nests, we found 1 extrapair young (4.2%) among totally 24 offspring.

Table 1. Number of broods sampled for paternity analysis, number of extrapair young (epy), and total number of adults present at the study site.

	1997	1998	1999	2000	2001	2002	2003
broods sampled	-	4	6	8	7	6	8
broods with epy		2	0	1	2	2	2
total number epy		3	0	1	3	2	2
% epy		20	0	3	14	10	6
adult males	30	26	40	44	41	37	23
adult females	20	24	25	26	24	19	18
% unpaired males	33	8	38	41	41	49	22
adult males / female	1.5	1.1	1.6	1.7	1.7	1.9	1.3

From 1997 – 2003, the mean proportion of unpaired males in our study population was 33 ± 14%, and the mean adult sex ratio was 1.5 ± 0.3 males per female. So far, we can say that it is not only males during their first breeding attempt that remained unpaired: out of 28 males that we captured in more than one year, four males were unpaired in the first year of capturing, five were unpaired in the second year, and one male was unpaired in both years. If we assume that the event of being unpaired is randomly distributed among males, the probability for a male to stay without a mate would be, on average, about 33% per year. In contrast, if we assume that the 7.5% extrapair young are randomly distributed among males, there would be only 0.37 extrapair young on average in each brood with five offspring. These possible sources of paternity loss compared, it appears that the variation in reproductive success that is caused by the male-biased sex ratio could be greater than the variation caused by extrapair fertilizations.

Furthermore, the operational sex ratio can be strongly male-biased also in a year when the adult sex ratio after settlement of all individuals is relatively even. It is the usual pattern that the first females arrive 1 – 3 weeks after the first males (Amrhein et al. 2002, 2004b). In 2003, for example (Fig. 1), the first females that arrived could potentially have chosen among many more than the 1.3 males per female that are indicated in Table 1: the three females that arrived on 19 April were faced with 19 males that had already occupied a territory, and females could potentially choose among males from the entire study site, since in several cases, females were found to settle in opposite corners of the area from one year to the next. Most females seem to decide where to settle within hours or one day from arrival and then are no longer available for other social mates: in 7 years of study, we only observed 1 female that remained unpaired and non-territorial for several consecutive days. If we assume that the females were ready to socially mate only during the day they arrived at the study site, while unpaired males were ready to mate until the end of the breeding season, this would result in a strongly male-biased operational sex ratio throughout the breeding season (Fig. 2), expressed as given by Kvarnemo & Ahnesjö (1996) as

males prepared to mate / (males + females prepared to mate)

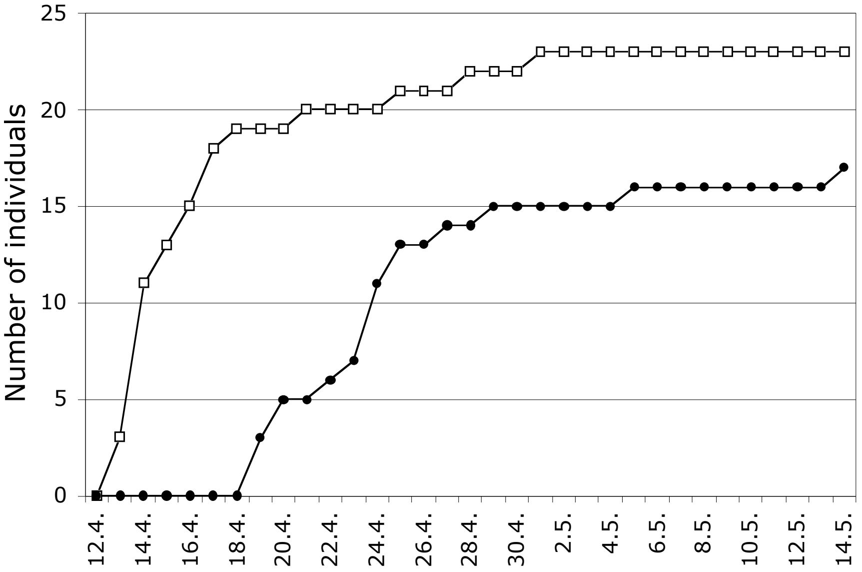

Figure 1. Number of territorial male (open squares) and female (closed circles) nightingales that have settled in the course of the breeding season 2003.

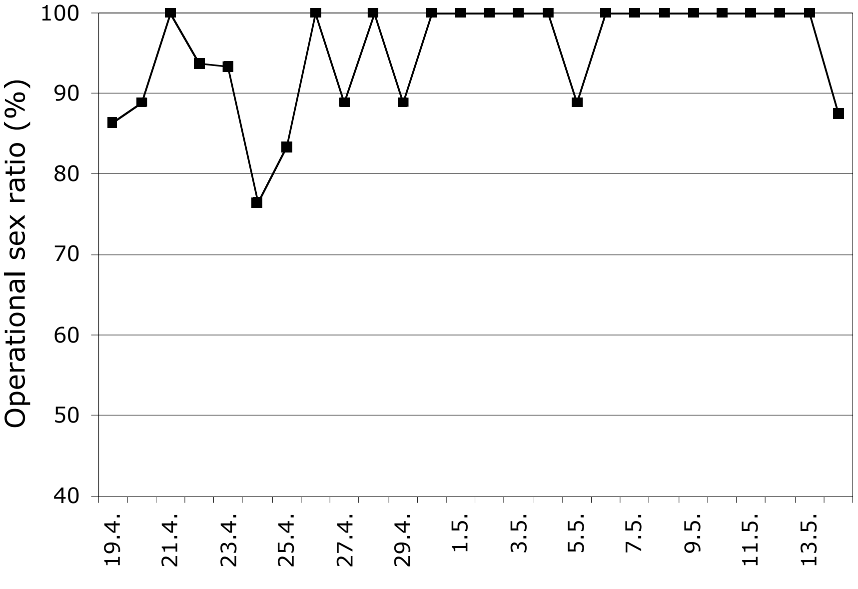

Figure 2. Operational sex ratio in the course of the breeding season 2003 (after Kvarnemo & Ahnesjö 1996), where 100% indicate that only males are ready to mate, while 0% would mean that only females are ready to mate.

Extraterritorial forays in males and females

The following paragraphs deal with the spatial behaviour of 10 radio-tagged nightingale couples studied in 2003. Males and females were tracked simultaneously, in up to three periods of the breeding cycle, for seven uninterrupted morning hours per period. For seven of the pairs, we collected blood samples (males no. 1 – 4 and 7 – 9; see Table 2). In the seven broods, we only found one extra-pair young (in the nest of male no. 8). None of the 10 females was found to visit other territories or to make excursions into unoccupied areas, in any of the three periods of the breeding cycle. Also the males (n = 8) did not leave their territories in the pre-laying period; in the laying period, however, five out of nine observed males made extraterritorial excursions, and all nine observed males visited other territories in the incubation period of their females (Table 2).

During the laying period, nine males spend 0 – 27% (9 ± 10%) of the tracking time outside their territories. The five males that left their territories made in total 24 excursions and entered 1 – 3 territories per excursion (1.2 ± 0.5). Out of the 28 territorial forays in the laying period, 20 forays were made into the territories of paired males, lasting for 12.3 ± 8.6 min per visit; 8 forays were made into territories of unpaired males, lasting for 9.2 ± 8.8 min per visit.

During the incubation period, nine males spend 1 – 25% (11 ± 9%) of the tracking time outside their territories. They made in total 20 excursions and entered 1 – 6 territories per excursion (1.6 ± 1.3). Out of the 32 territorial forays in the incubation period, 25 forays were made into the territories of paired males, lasting for 11.2 ± 10.7 min per visit, and 7 forays were made into territories of unpaired males, lasting for 4.3 ± 3.7 min per visit. During the incubation period, male no. 9 made two additional excursions into an unoccupied territory in 180 m distance, where it also was heard singing.

Only two males made forays into a territory of a fertile female that had not yet begun with egg-laying or incubation. However, during three forays, two intruding males were found to visit the nest of an incubating female, and during at least 13 forays the intruding males (n = 9) closely approached the singing resident male.

Table 2. Extra-territorial excursions of 10 male nightingales, within 7 morning hours per period of their females' breeding cycle. After each separate excursion, the males returned to their own territories. The days of data collection in the pre-laying period are numbered relative to the laying of the first egg; laying day no. 1 is when the first egg was laid, and incubation day no. 1 is the day after the last egg was laid.

Male No.	Day	No. separate excursions	Max. distance to own territory	Time (min) outside occupied territories	Time (min) inside occupied territories	No. of different visited territories	Breeding stage in visited territories (day)
Pre-laying period							
1	-1	-					
2	-1	-					
3	-2	-					
4	-3	-					
5	-2	-					
6	-3	-					
7	-5	-					
(8)							
(9)							
10	-4	-					
Laying period							
1	3	-					
2	3	2	50	-	38	2	laying (4)
3	4	-					
4	2	9	70	-	86	2	pre-lay. (-2)
5	3	-					
6	4	4	260	-	114	2	laying?
7	5	-					
8	1	4	50	-	26	1	pre-lay (-1)
(9)							
10	1	5	80	4	56	3	laying?
Incubation period							
1	4	1	290	8	46	3	incub.
2	5	1	70	-	8	1	incub.
3	5	2	320	8	96	4	incub.
4	6	1	20	-	6	1	unpaired male
5	8	2	252	-	26	3	incub.
6	3	4	102	8	20	2	incub.?
7	6	1	50	-	30	1	incub.?
8	9	6	60	-	52	1	incub.
9	7	4	186	78	26	2	incub.
(10)							

Intrapair distances and male singing activity

Singing activity was measured as the proportion of radio fixes (excluding extraterritorial excursions) that a male sang. The seven males that were tracked during all three periods of the breeding cycle sang more in the laying period than in the pre-laying or incubation periods (Fig. 3). This pattern was not significant (Friedman test, $n = 7$, d.f. = 2, $p = 0.16$), but it was consistent with our previous findings (Amrhein et al. 2002, 2004b). The proportion of radio fixes that the pair members were close to each other (within 8 m distance) decreased sharply from the pre-laying to the laying period (Fig. 3; Friedman test, $n = 7$, d.f. = 2, $p = 0.006$).

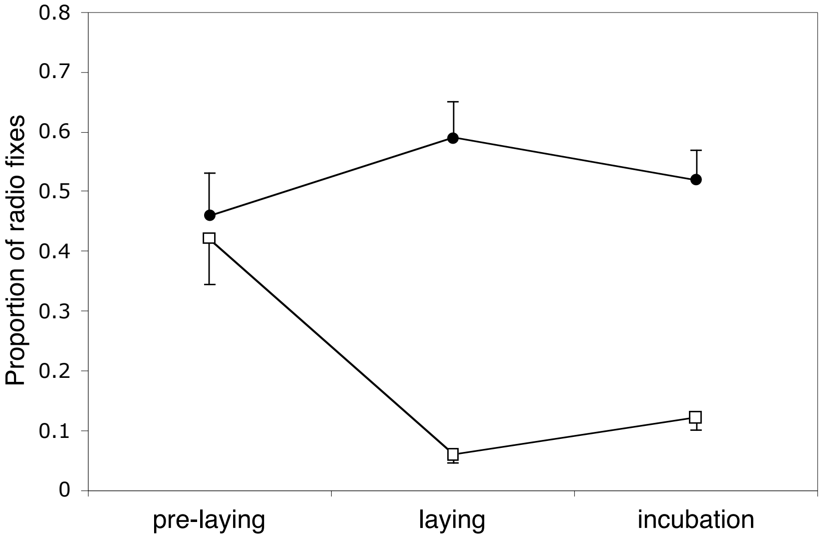

Figure 3. Closed circles: mean ± *s.e.* singing activity of seven males, expressed as the proportion of radio fixes that a male was heard singing. Open squares: mean ± *s.e.* proportion of radio fixes that the members of seven pairs were close to each other (within 8 m distance).

In the pre-laying period, the proportion of time the pair members were closely associated varied greatly between pairs and between days of data collection (Fig. 4a). On day –3 before the first egg was laid, male no. 6 was during 75% of the radio fixes close to its mate, but on the same day, another pair was much less closely associated. We also found no linear relationship between the day before egg-laying and association of the pair members (linear regression, $r^2 = 0.06$, $F_{1,6} = 0.36$, $p = 0.57$). In the egg-laying period, however, two pairs were together during 18% and 29% of the radio fixes on the day the first egg was laid, and as the clutch size increased, the other pairs were less closely associated (Fig. 4b; linear regression, r^2

= 0.60, $F_{1,7}$ = 10.59, p = 0.01). In the incubation period, there was again considerable variation between pairs, and we found no clear trend as the season progressed (Fig. 4c; linear regression, r^2 = 0.05, $F_{1,7}$ = 0.35, p = 0.57).

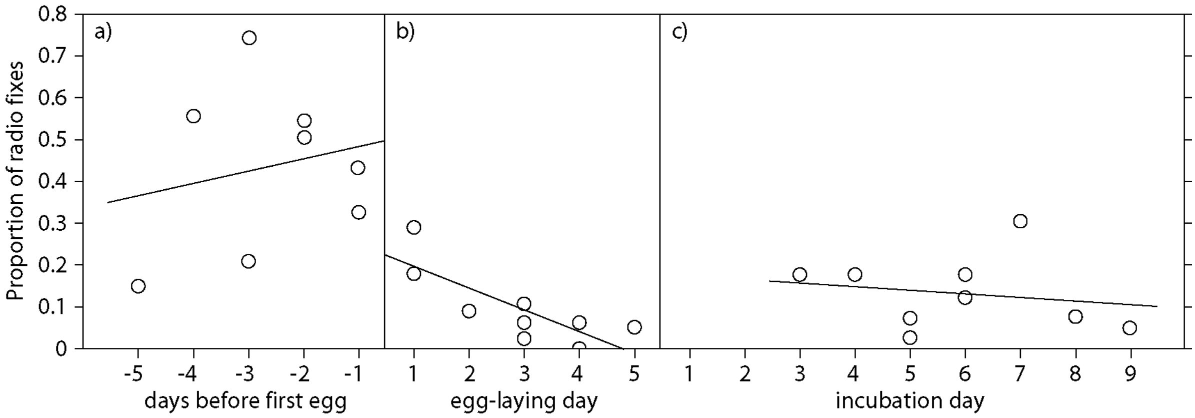

Figure 4. Proportion of radio fixes that the members of a) 8 pairs, b) 9 pairs, and c) 9 pairs were close to each other (within 8 m distance).

For the radio fixes with maximal 8 m intrapair distance, we analysed whether it was the male or the female that had approached the other mate. In the pre-laying period, the males (n = 8) approached the females for 38 – 70% (54 ± 11) of the radio fixes, whereas the females approached the males for 30 – 63% (46 ± 11) of the fixes. These findings indicate that the males made no special effort to pursue their females, but that it was also often the females that approached their males.

Corresponding to the proportional values of intrapair distances, the mean number of metres between pair members was lowest in the pre-laying period and greatest in the laying period (Fig. 5). This pattern was found for both the radio fixes at which the male was singing (Friedman test, n = 7, d.f. = 2, p = 0.01) and the fixes without song (Friedman test, n = 7, d.f. = 2, p = 0.002). When we pooled the data from all three periods, the males (n = 7) were on average further from their mates while singing (53 ± 27 m) and closer to their mates while not singing (35 ± 11 m; Wilcoxon signed ranks test, Z = -2.37, n = 7, p = 0.018).

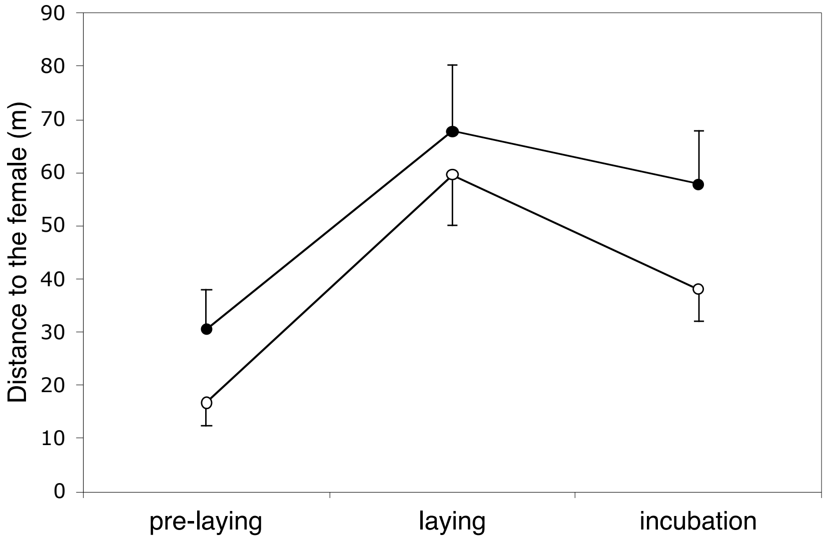

Figure 5. Mean ± *s.e.* distance between the members of seven pairs. Closed circles are radio fixes at which the male was singing, open circles are radio fixes of the non-singing male.

Discussion

In this study, we found a relatively low rate of extrapair fertilization in the nightingale. However, the adult sex ratio was strongly male-biased for several years, and the operational sex ratio remained male-biased throughout the breeding season. These sex ratios could potentially lead to a greater variation in reproductive success and cause more competition among males than we would expect to result from the rate of cuckoldry.

Accordingly, we found no distinct extrapair behaviour in male and female nightingales. Males did not pursue their females nor did they sing at elevated levels during the days before egg-laying. Pair members were close to each other to varying but, on average, low degrees before egg-laying and showed great intrapair distances once egg-laying had started. Females were not found to visit other territories, and males made excursions only after egg-laying had begun, to visit mostly territories where the females were already incubating.

Extrapair paternity and mate guarding

Among 147 nestlings, we found 7.5% that were sired by an extrapair male. This is a moderate frequency of extrapair fertilization, as compared to the mean of 17.6% extrapair young that was given in a recent compilation of studies on 73 passerine species (Wink & Dyrcz 1999). In particular, the occurrence of cuckoldry was low as compared to the closely related bluethroat (*Luscinia svecica*), where a frequency of 30% extrapair young was found (Johnsen et al. 1998). In the bluethroat, males show close mate guarding by following the movements of the females, and on the two days before egg-laying commences, they spend on average over 60% of the time closer than 1 m to their mate (Krokene et al. 1996). In contrast, nightingale pair members were within 8 m distance to each other for, on average, 42% of the time in the five days before egg-laying, and proximity to the mate was initiated to a similar degree by both pair members. Although the different pairs varied greatly in the proportion of time they spent together, we do not expect that closely following the female is a paternity defence strategy that is often applied by male nightingales. We also doubt this strategy is useful in the extremely dense bushes where nightingales usually stay; the female could easily escape the male paternity guards, especially when it is closely guarded for only 42% of the time. Furthermore, it may not have been necessary to guard the females, because, among the territories where we examined intrapair distances, only one out of seven nests contained one extrapair young.

The fertile period and singing activity

Rather, the male may be closely associated to the female for some proportion of the time before egg-laying in order to frequently copulate with her. This is a paternity defence strategy that is thought to be important in monogamous bird species in which mate guarding by close following does not occur (Birkhead 1998). However, our data suggest that copulations became less frequent after the first egg was laid, since the proportion of time that the pair members were close to each other decreased to low levels once egg-laying started. Indeed, it is known for many species that intrapair copulations peak about three days before the first egg is laid and then become less frequent or even absent after laying of the first egg, and this applies also to extrapair copulations and related behaviour (Westneat 1987; Arvidsson 1992; Birkhead & Møller 1993; Sheldon & Burke 1994). Although copulations could potentially lead to fertilization until the last egg is ovulated, it appears that, in species with low levels of extrapair fertilization like the nightingale, the behaviour of males during egg-laying of their mates is less closely related to female fertility than before. In the nightingale, singing activity is low when presumably most copulations take place, that is, during the three days before egg-laying starts, but it reaches a peak during egg-laying (Amrhein et al. 2004b). Thus, song does not seem to be important as a paternity guard in the nightingale. Our study also does not support the hypothesis that song during egg-laying is mainly directed to the mate, e. g. to encourage her to increase the investment in the brood according to male quality (Amrhein et al. 2002). During egg-laying, we measured the greatest values of intrapair distance, and throughout the breeding cycle the male was further from its mate while singing than while not singing. We therefore suggest that the high singing activity during egg-laying is directed to recipients outside the territory, that is either to females seeking extrapair copulations or to other males.

Extra-territorial excursions

Of course, the fact that we did not observe females visiting other territories does not mean that female nightingales never leave the territory to solicit extrapair copulations. It may well be that those females that had extrapair young in the nest in fact made extraterritorial excursions. In species with more elevated levels of cuckoldry, like the bluethroat, the hooded warbler (*Wilsonia citrina*), or the superb fairy-wren (*Malurus cyaneus*), fertile females are regularly found to visit extrapair males, and these visits also lead to extrapair fertilizations (Smiseth & Amundsen 1995; Neudorf et al. 1997; Double & Cockburn 2000). In the hooded warbler, also the males visit other territories, and they do so when their females are in the pre-laying, laying or incubation periods, while during their excursions, they visit predominantly fertile females (Stutchbury 1998). In contrast, male chaffinches (*Fringilla coelebs*) make more extra-territorial excursions when their mates are incubating than before, and they do not selectively visit fertile females (Hanski 1992), but are often found to forage outside occupied territories and in territories of other males (Maciejok et al. 1995). In the nightingale, males often visited other territories and approached the singing males, but only rarely spent time in unoccupied areas. We doubt that the main function of male extraterritorial excursions was to forage, since food was probably also abundant outside nightingale territories. Males left their territories only when their females were egg-laying or incubating, and they visited mostly territories in which the females were incubating. Thus, the timing of their extra-territorial excursions apparently was not optimised if the main function was to obtain extrapair copulations. In our study population, the egg-laying periods were strongly synchronized, but the males were not found to visit other fertile females during the pre-laying period of their mates, although they should have had time to do so: the males spent on average less than half of the time close to their mates during the pre-laying period. Therefore, we do not expect that males stayed in their territory because of a trade-off between mate guarding and pursuing extrapair copulations (Stutchbury 1998; Chuang-Dobbs et al. 2001). In later periods of the breeding cycle, males may have forayed into other territories to obtain extrapair fertilizations in replacement clutches. However, in 8 replacement nests, we found only 1 extrapair young (4.2% of the offspring in replacement broods). In conclusion, we suggest that possible extrapair behaviour is under female control in the nightingale, and that male extra-territorial excursions mainly serve other functions than extrapair fertilization or foraging.

Adult sex ratio and territorial behaviour

The nightingale is a strictly territorial species. At least for some part of the breeding season, all males defend a territory (Amrhein et al. 2004a), and this territory, as in most songbirds, seems to be an essential prerequisite for the attraction of a female (Catchpole & Slater 1995). However, each year there were many males that remained unpaired in our study population, and the operational sex ratio was male-biased throughout the breeding season. Males should therefore intensely compete for territories and mates (Kvarnemo & Ahnesjö 1996). In the course of the breeding season, some unpaired males usually leave their territories to prospect the area; during the inspection trips, unpaired males often sit close to singing males and spend more time in territories where a female is present than in territories of unpaired males (Amrhein et al. 2004a). So far, we only have little evidence that territory prospecting of unpaired males is followed by successful breeding in the subsequent year: in 2002, one unpaired male left its territory and settled in a new territory in 500 m distance on the day the paired resident died; in 2003, the male bred successfully in the new territory with a new female. In the present study, paired males showed similar behaviour as unpaired males, by prospecting other territories, often approaching the singing residents, and spending more time in territories of paired males than of unpaired males, although in the visited territories most females were already incubating. We suggest that a large proportion of singing and extra-territorial activity of males after their mates' fertile period functions in male-male competition. A main purpose of extra-territorial excursions may be to gather information on territory occupancy by males and females (Hanski 1992; Amrhein et al. 2004a), or to explore social relationships among neighbours (Naguib et al. 2004). This information may be vital for defending the own territory in the current season and to succeed in competition for territories and social mates in the next breeding season. Furthermore, 24% of male nightingales have been shown to change the territory from year to year (Grüll 1981), and the decision where to settle in the next season may also be influenced by information obtained during extra-territorial excursions in the current season (Doligez et al. 2004).

For largely unknown reasons, there seems to be a male-biased adult sex ratio in many bird species (Breitwisch 1989). In recent years, there is growing interest in the ability of birds to control the sex of their offspring (Komdeur et al. 2002; Cockburn et al. 2002). Skewed adult sex ratios, however, can also arise in populations where the sex ratio at birth is balanced (Breitwisch 1989). The implications of skewed adult sex ratios in birds are so far largely unexplored. Few recent studies have suggested that a male-biased adult sex ratio could substantially contribute to the evolution of sexual ornaments in monogamous bird species, at least in cases where extrapair fertilization is not likely to be the main source of variation in male reproductive success (Hill et al. 1994; Dearborn et al. 2001). Here, we intended to point to the potential of adult sex ratios in influencing behavioural traits that are commonly interpreted to function in sperm competition. In the nightingale, we found low levels of extrapair fertilization, and frequent extra-territorial excursions of males could be related to competition for territories and ultimately to competition for social mates. Low levels of paternity insurance behaviour but marked territory defence activity are also found in other monogamous species exhibiting male-biased adult sex ratios like the robin (Tobias & Seddon 2000). It remains to be shown if variation in reproductive success caused by a male-biased adult sex ratio is non-randomly distributed with respect to spatial behaviour and exaggerated traits like bird song and therefore plays a role in sexual selection of these traits.

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V

Bestand und Verpaarungsstatus von Nachtigallen *Luscinia megarhynchos* im elsässischen Rheintal bei Basel

Valentin Amrhein und Daniel Zwygart

Population size and mating status of Rufous Nightingales *Luscinia megarhynchos* in the Upper Rhine Valley near Basel. – In 2003, we censused singing Rufous Nightingales in a study area of 17.9 km^2 between Saint-Louis and Kembs-Loechlé (France). Three surveys were made during the day and one at night. We counted 194 singing males, 83 of which were heard only during the day, 38 only at night, and 73 bothat day and night. Since male Nightingales usually stop singing at night after pairing, we suggest that the 111 nocturnal singers were mostly unpaired males, while the minimum number of paired males would be 83. However, Nightingales were less easily heard during the day than at night. Based on the results from an intensively examined part of the study area (the Petite Camargue Alsacienne), we assume that the actual number of paired males was higher than 83 and that the population size was up to 240 males, about half of them being unpaired. We suggest that the high proportion of unpaired males reflects a strongly male-biased adult sex ratio and discuss implications for sexual selection and the interpretation of bird census data.

Key words: *Luscinia megarhynchos*, population size, mating status, bird census, Upper Rhine Valley.

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Die Anwesenheit männlicher Nachtigallen ist auch in grossen, unübersichtlichen Gebieten leicht festzustellen. Die einfachste Methode sind Ende April und Anfang Mai gegen Mitternacht durchgeführte Kontrollen. Unverpaarte ♂ singen fast jede Nacht; der Gesang ist in freiem Gelände etwa 500 m weit zu hören und auch von Laien gut zu erkennen. Nach der Verpaarung wird der Nachtgesang eingestellt; nur während die ♀ Eier legen, beginnt ein Teil der verpaarten ♂ erneut für durchschnittlich drei bis vier Nächte zu singen (Amrhein et al. 2002, 2004). Um die verpaarten ♂ zu erfassen, müssen also auch Tageskontrollen durchgeführt werden. Im Morgenchor und tagsüber singen unverpaarte und verpaarte ♂ ähnlich häufig (Amrhein et al. 2004). Weil die Nachtigall tagsüber wegen des erhöhten Lärmpegels weniger hervorsticht, sind dann allerdings mehr Kontrollen nötig als nachts. Führt man die nächtlichen Kartierungen nach Ankunft und Eiablage der ♀ durch, so lässt sich aus dem Verhältnis von nachts singenden zu tagsüber singenden ♂ abschätzen, wie hoch der Anteil unverpaarter ♂ in einer Population ist. Dies gibt uns ein einmaliges Werkzeug an die Hand, um bei einer Singvogelart zu evaluieren, wie viel die Anzahl grossflächig kartierter Gesangsreviere über den tatsächlichen Brutbestand aussagt.

Obwohl Nachtigallkartierungen leicht durchführbar und wegen des nächtlichen Naturerlebnisses auch besonders eindrucksvoll sein können, sind grossflächige Erhebungen selten. Die meisten bisherigen Revierkartierungen betrafen Gebiete mit Flächen um 200 ha bis maximal 600 ha (Zusammenstellungen in Glutz von Blotzheim & Bauer 1988, Schmid et al. 1998, Hölzinger 1999).

In der vorliegenden Studie haben wir mit einfacher Methodik die Anzahl singender Nachtigallen und ihren wahrscheinlichen Verpaarungsstatus im elsässischen Rheintal unmittelbar nördlich von Basel erfasst. Bei einer früheren Zählung am 20. Mai 1990 wurden in dieser Gegend auf ca. 100 km^2 französischem und deutschem Gebiet 267 singende ♂ gehört (Berger 1990). In unserer Studie haben wir uns auf denjenigen Bereich konzentriert, in dem damals die meisten Nachtigallen gefunden wurden.

Abb. 1. Typisches trockenes Nachtigallenbiotop in der Petite Camargue Alsacienne. Das Nest befand sich in der Krautschicht am Waldrand. – *Typical dry Nightingale habitat in the Petite Camargue Alsacienne. The nest was in the herbage at the edge of the wood.*

1. Methode

Unser Zählgebiet war 17,9 km^2 gross und lag zwischen den Ortschaften Saint-Louis und Kembs-Loechlé (Abb. 2). Im Zentrum des Zählgebietes befindet sich die Petite Camargue Alsacienne, in der wir seit 1994 den Nachtigallenbestand untersuchen (Durrer et al. 1995, Amrhein et al. 2002, 2004). Die Zählungen wurden von 22 Schülerinnen und Schülern im Alter von etwa 17 Jahren durchgeführt. Wir unterteilten das Zählgebiet in fünf Teilgebiete, die von je einer Schülergruppe (jeweils 4 bis 5 Schüler) dreimal mit dem Velo abgefahren wurden. Die Routen waren so gewählt, dass alle für Nachtigallen geeigneten Biotope abgehört werden konnten. Alle singenden Nachtigallen wurden in Karten eingetragen. Wir haben die Schüler vor der Kartierung anhand von Tonbandaufnahmen und im Freiland mit dem Nachtigallengesang vertraut gemacht. Die Zählungen fanden statt am 7. Mai 2003 von 17.00 bis 20.00 Uhr, in der Nacht vom 7. auf den 8. Mai von 23.00 bis 01.00 Uhr sowie am 9. Mai von 05.00 bis 07.00 Uhr. In die Auswertung wurde auch eine ganztägige Vorexkursion vom 24. April (D. Zwygart) einbezogen, so dass der Datensatz insgesamt drei Tageszählungen und eine Nachtzählung umfasst.

Zusätzlich haben wir in der Brutsaison 2003 den exakten Bestand von Nachtigallen auf 122 ha in der Petite Camargue ermittelt. Dort sangen 28 revierbesitzende Nachtigall-♂ (2,3 Reviere pro 10 ha), von denen acht (29 %) unverpaart blieben. Die 28 ♂ besetzten ihre Reviere zwischen dem 13. April und 1. Mai (Mittelwert ± Standardabweichung: 17. April ± 5 Tage). Zwischen dem 15. und 28. April sangen ausserdem in zehn unbesetzten Revieren für meist nur einen Tag ♂, die entweder umher schweifende Nachtigallen der Petite Camargue oder Durchzügler gewesen sein können. Wir gehen davon aus, dass der Durchzug am 7. bis 9. Mai bereits beendet war und die singenden Nachtigallen im gesamten Zählgebiet revierbesitzende ♂ waren. In 18 Revieren der Petite Camargue konnten wir feststellen, dass sich die ♀ zwischen dem 19. April und 14. Mai ansiedelten (25. April ± 6 Tage), wobei sich im Mai nur zwei verspätete ♀ am 5. und 14. Mai in einem Revier niederliessen. In zehn genau kontrollierten Nestern der Petite Camargue wurde das jeweils letzte Ei zwischen dem 4. und 8. Mai gelegt (5. Mai ± 1 Tag). Wir nehmen daher an, dass bei unserer Nachtzählung am 7./8. Mai in einem Grossteil der Reviere des Zählgebietes die ♀ bereits brüteten und die verpaarten ♂ nachts nicht mehr sangen.

2. Ergebnisse

Bei den vier Zählungen wurden insgesamt 194 singende Nachtigallen kartiert. Zusammen mit acht bei den Zählungen nicht kontrollierten Revieren aus der Petite Camargue betrug der Mindestbestand im Zählgebiet 202 singende ♂. Die Nachtigallen waren flächendeckend in geeigneten Biotopen verbreitet und fanden sich vor allem entlang des Rheins, entlang des bei Huningue abzweigenden Kanals und entlang der Niederterrassenkante, sowie in der Petite Camargue und um die westlich daran angrenzenden Kiesgruben (Abb. 1).

Anhand des genau untersuchten Nachtigallenbestandes der Petite Camargue konnten wir die Zählgenauigkeit überprüfen. Von den neun in jener Nacht singenden Nachtigallen der Petite Camargue, die auf der Zählroute der Schüler lagen, wurden alle bei der Nachtzählung gehört; zwei davon wurden nur in der Nacht, nicht aber tagsüber gehört. Von 12 nur tagsüber singenden ♂ der Petite Camargue wurde eines bei keiner der drei Tageszählungen gehört. Dies bestätigt, dass bereits vier Zählungen ausreichen, um einen Nachtigallenbestand relativ genau zu erfassen; es zeigt sich aber, dass es wahrscheinlicher ist, eine Nachtigall nachts zu hören als tagsüber.

Bei den vier Zählungen wurden 83 ♂ nur tagsüber gehört; dies waren mit grosser Wahrscheinlichkeit verpaarte ♂. 111 ♂ wurden nachts gehört, davon 38 nur nachts und 73 sowohl nachts als auch tagsüber. Nur 66 % der Nachtsänger wurden also auch tagsüber gehört. Gehen wir davon aus, dass von den reinen

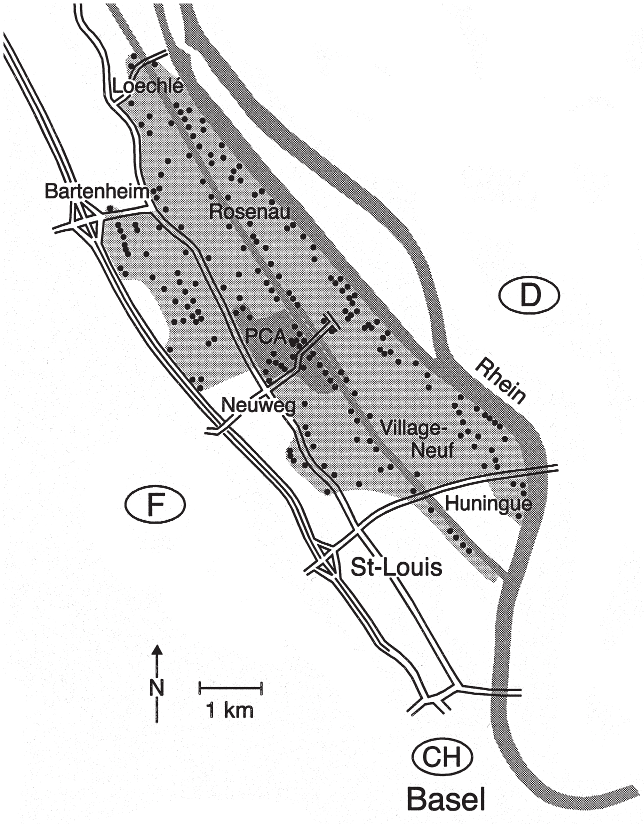

Abb. 2. Das Zählgebiet der Nachtigallkartierung 2003 (hellgrau) mit der Petite Camargue Alsacienne (PCA) im Zentrum. Als Punkte dargestellt sind 194 revieranzeigende ♂ und zusätzlich 8 Reviere in der Petite Camargue, die nicht auf der Zählroute lagen. – *Study area (light grey) with the Petite Camargue Alsacienne (PCA). Dots are 194 singing Nightingales and 8 additional territories in the Petite Camargue that were not monitored during the four censuses.*

Tagsängern ebenfalls nur 66 % gehört wurden, so ergäbe sich bei 83 nur tagsüber gehörten ♂ eine hypothetische Anzahl von 126 reinen Tagsängern. Mit dieser Hochrechnung kämen wir auf insgesamt 237 ♂; der Anteil unverpaarter ♂ läge dann mit 111 nachts singenden ♂ bei 47 %.

3. Diskussion

Insgesamt schätzen wir den Bestand auf 200 bis 240 revierbesitzende Nachtigall-♂, von denen rund die Hälfte nachts sang und vermutlich unverpaart war. Der geschätzte Anteil von 47 % unverpaarten ♂ mag etwas zu hoch gegriffen sein, da unter den Nachtsängern wahrscheinlich auch verpaarte ♂ waren, deren ♀ noch nicht alle Eier gelegt hatten, die nach Beginn der Bebrütungsphase noch einzelne Nächte sangen (Amrhein et al. 2002, 2004) oder bei denen sich erst nach unserer Zählung ein verspätetes ♀ ansiedelte. Ein solcher Prozentsatz unverpaarter ♂ entspricht jedoch unserer Erfahrung aus der Petite Camargue: Im Jahre 2002 zum Beispiel blieben dort 21 von 43, also 49 % der ♂ unverpaart (Amrhein et al. 2003).

Da wir zwischen 1997 und 2003 in der Petite Camargue nur ein einziges definitiv unverpaartes ♀ fanden, gehen wir davon aus, dass es bei den adulten Nachtigallen der Rheinebene bei Basel aus noch unbekannten Gründen einen starken ♂-Überschuss gibt. Das könnte ein weit verbreitetes Muster sein: In vielen Gegenden Europas kann man nachts singende Nachtigallen auch spät in der Brutsaison antreffen.

Auch bei anderen Singvogelarten ist ein ♂-Überschuss unter den Altvögeln bekannt (Breitwisch 1989). Beim nordamerikanischen Hausgimpel *Carpodacus mexicanus* betrug der Anteil unverpaarter ♂ in fünf verschiedenen Populationen je 7, 31, 34, 53 und 58 % aller ♂ (Hill et al. 1994). Gibt es in einer Population mehr adulte ♂ als ♀, so kommt es auch bei sozial und sexuell eher monogamen Arten wie dem Hausgimpel (Hill et al. 1994) oder der Nachtigall (Amrhein 2004) zu starker Varianz im Fortpflanzungserfolg der ♂. Die Konkurrenz unter den ♂ und das Wahlverhalten der ♀ können dann verstärkt zur Selektion von Merkmalen führen, die den Paarungserfolg direkt beeinflussen, wie zum Beispiel auffällige Balzfärbung oder variationsreicher Gesang (Hill et al. 1994, Amrhein 1999, Ligon 1999).

♂ konkurrieren nicht nur direkt um ♀, sondern auch um Reviere, die für die längerfristige Bindung eines ♀ unerlässlich sind (Catchpole & Slater 1995). Die Anwesenheit vieler unver-

Abb. 3. Typisches feuchtes Nachtigallenbiotop. Das Nest befand sich in den Brennesseln am rechten Bildrand. – *Typical humid Nightingale habitat. The nest was in the nettles on the right.*

paarter und eventuell das Revier wechselnder ♂ kann auch Auswirkungen auf den Reviergesang haben: Wir konnten zeigen, dass sich unverpaarte und zeitweise revierlose ♂ besonders in der Stunde vor Sonnenaufgang frei im Gebiet bewegen und besetzte Reviere erkunden. Dies kann ein Grund dafür sein, warum bei der Nachtigall ebenso wie bei anderen Vogelarten die revierbesitzenden ♂ in der Morgendämmerung am meisten singen und somit ihr Revier markieren (Amrhein et al. 2003).

Für die Feldornithologie bedeutet ein hoher Prozentsatz unverpaarter ♂, dass man nicht ohne weiteres von der Anzahl Gesangsreviere auf die Anzahl Brutpaare schliessen kann. Die Brutbestände auch mancher anderer Arten könnten weitaus kleiner sein, als es die Zählungen singender ♂ vermuten lassen.

Die von uns kartierten 200 bis 240 Nachtigall-♂ sangen auf einer Fläche von 1790 ha; das ergibt eine Siedlungsdichte von 1,1 bis 1,3 Revieren pro 10 ha, was etwa den Ergebnissen von anderen mitteleuropäischen Zählungen in geeigneten Landschaften entspricht (Glutz von Blotzheim & Bauer 1988). Eine der grossflächigsten uns bekannten Erhebungen fand am oberen Genfersee-Ende statt: Gilliéron (1991) schätzt für eine Fläche von ca. 6 km^2 die Anzahl der zwischen 1979 und 1988 regelmässig besetzten Reviere auf 65 bis 70, was 1,1 bis 1,2 Reviere pro 10 ha ergibt. In den südlich unseres Zählgebietes liegenden Kantonen Basel-Landschaft und Basel-Stadt sind dagegen seit den Dreissigerjahren des letzten Jahrhunderts nur vereinzelte Nachtigallen zu hören gewesen (Blattner & Kestenholz 1999). Wir finden es erstaunlich, dass im unmittelbar angrenzenden Ausland auf einer Untersuchungsfläche von knapp 18 km^2 ein Nachtigallenbestand anzutreffen ist, der einem Zehntel des Schweizer Gesamtbestandes (2000 bis 2500 Reviere) entspricht; wir hoffen mit Schmid et al. (1998), dass die Renaturierung von Fliessgewässern (Abb. 3), Heckenlandschaften und unterholzreichen Waldrändern (Abb. 1) die Situation für die Nachtigall auch in der Schweiz verbessern wird.

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Zusammenfassung, Résumé

Im Frühjahr 2003 haben wir auf einer Fläche von 17,9 km^2 zwischen Saint-Louis und Kembs-Loechlé (Frankreich) den Bestand singender Nachtigallen erfasst. Tagsüber wurden drei Zählungen durchgeführt, und eine Zählung erfolgte nachts. Wir kartierten 194 singende ♂, von denen 83 nur tagsüber gehört wurden, 38 nur nachts, und 73 sowohl tagsüber als auch nachts. Da Nachtigall-♂ nach der Verpaarung meistens aufhören, nachts zu singen, nehmen wir an, dass die 111 Nachtsänger grösstenteils unverpaarte ♂ waren; die Mindestanzahl verpaarter ♂ wäre dann 83. Allerdings war die Erfassung singender ♂ tagsüber weniger genau als nachts. Basierend auf den exakten Bestandszahlen aus einem intensiv untersuchten Teilgebiet (der Petite Camargue Alsacienne) folgern wir, dass die tatsächliche Anzahl verpaarter ♂ grösser war als 83 und schätzen den Gesamtbestand auf 200–240 revierbesitzende ♂, von denen rund die Hälfte unverpaart war. Wir nehmen an, dass die grosse Anzahl unverpaarter ♂ tatsächlich einen starken ♂-Überschuss widerspiegelt und diskutieren dessen Bedeutung für die sexuelle Selektion und die Interpretation von Bestandserfassungen durch Revierkartierung.

Etat de la population et statut de l'appariement du Rossignol philomèle *Luscinia megarhynchos* dans la vallée du Rhin, en Alsace, près de Bâle

Au printemps 2003, nous avons recensé les mâles chanteurs de Rossignol philomèle sur une surface de 17,9 km^2 entre Saint-Louis et Kembs-Loechlé (France). Nous avons réalisé trois comptages pendant la journée et un comptage pendant la nuit. Nous avons compté 194 mâles chanteurs, dont 83 entendus seulement pendant la journée, 38 seulement pendant la nuit, et 73 pendant la journée et la nuit. Comme les rossignols mâles s'arrêtent habituellement de chanter la nuit juste après l'accouplement, nous pensons que la majorité des 111 mâles qui ont chanté pendant la nuit étaient des mâles non appariés; le

nombre d'individus appariés serait alors de 83 au minimum. Cependant, il était moins facile de repérer un rossignol chantant pendant la journée que pendant la nuit. En nous appuyant sur les données précises d'un secteur intensivement étudié (la Petite Camargue Alsacienne), nous estimons que le nombre véritable de mâles appariés était de plus que 83 et que la population totale était de 200 à 240 mâles cantonnés, dont la moitié était non appariés. Nous pensons que le grand nombre de mâles non appariés laisse supposer qu'il y a beaucoup plus de mâles que de femelles. Nous en discutons des implications pour la sélection sexuelle et pour l'interprétation des données obtenues par des recensements de mâles chanteurs.

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Anhang

Vegetation und Landschaftsstrukturen
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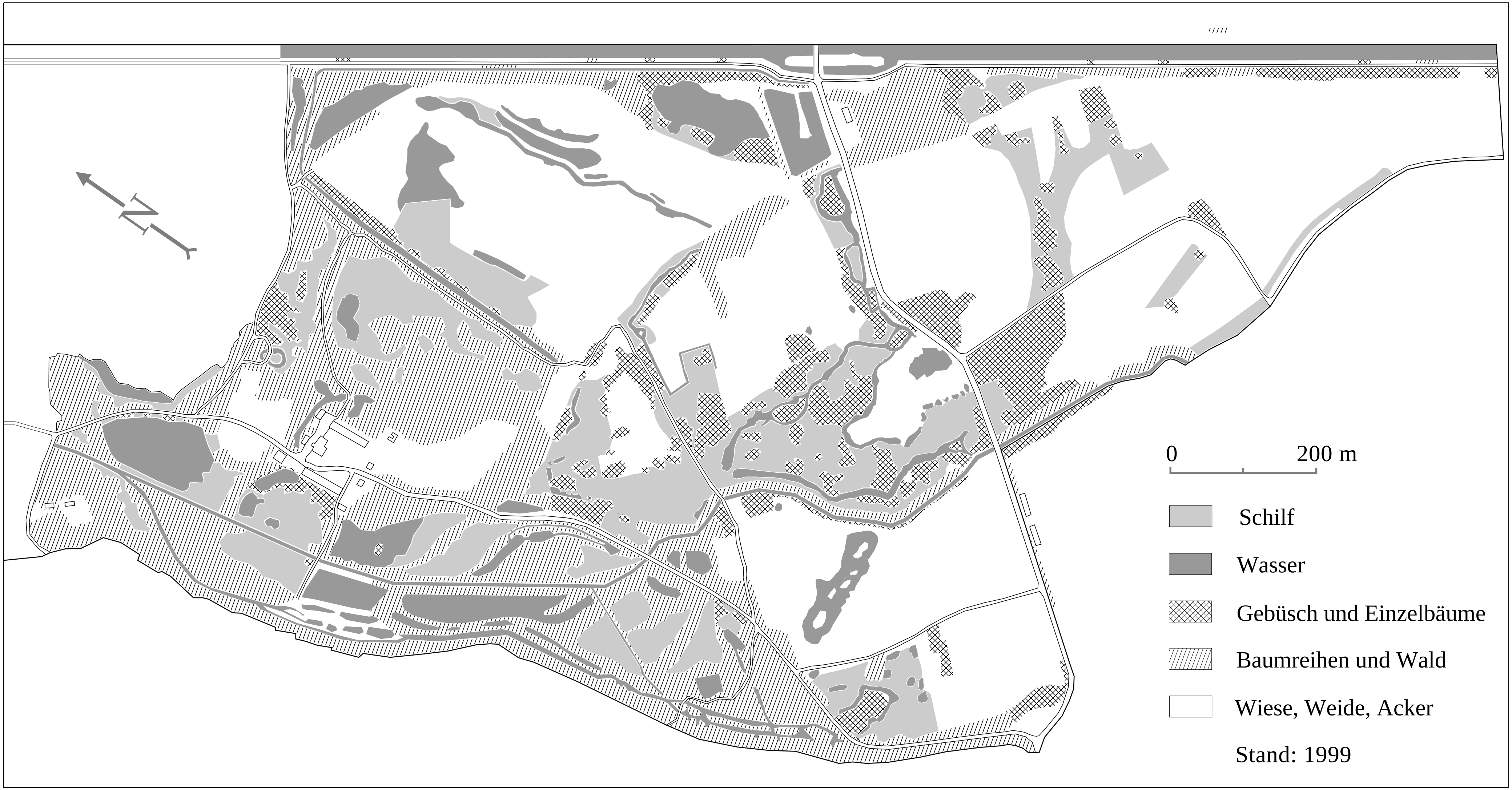

Arbeitsteilung der Autoren

I. Amrhein, V., Korner, P. & Naguib, M. (2002) Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. Anim. Behav.
Idee, Durchführung und Niederschrift von V. Amrhein; P. Korner und M. Naguib halfen bei Auswertung und Fertigstellung des Manuskriptes.

II. Amrhein, V., Kunc, H. P. & Naguib, M. (2004) Seasonal patterns of singing activity vary with time of day in the nightingale. Auk.
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III. Amrhein, V., Kunc, H. P. & Naguib, M. (2004) Non-territorial nightingales prospect territories during the dawn chorus. Proc. R. Soc. Lond. B (Suppl.).
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IV. Amrhein, V., Kunc, H. P. & Naguib, M. (Manuscript) Sperm competition or sex ratio: Possible factors influencing singing and spatial behaviour in the nightingale.
Idee, Feldarbeit und Niederschrift von V. Amrhein; H. Kunc und M. Naguib organisierten die Vaterschaftsanalysen; H. Kunc schrieb den Methodenteil der Vaterschaftsanalysen.

V. Amrhein, V. & Zwygart, D. (2004) Bestand und Verpaarungsstatus von Nachtigallen im elsässischen Rheintal bei Basel. Ornithol. Beob.
Idee von H. Durrer & V. Amrhein; Durchführung von D. Zwygart & V. Amrhein; Auswertung und Niederschrift von V. Amrhein.

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Kunc, H. P., Amrhein, V. & Naguib, M. (submitted): Seasonal variation of dawn song and its relation to pairing success in the nightingale.

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