Declivi de la trenca (*Lanius minor*) al límit de l'àrea de distribució: causes, mecanismes i propostes de conservació

Decline of the Lesser Grey Shrike (*Lanius minor*) at the western limit of the distribution area: causes, mechanisms and conservation proposals

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A l’avi Joan i a la meva mare
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INTRODUCCIÓ GENERAL

Canvi global i pèrdua de biodiversitat

El canvi global és un procés de canvi o de transformació a escala planetària derivat de l'activitat humana, que inclou tot una sèrie forces com ara el canvi climàtic, el canvi dels usos del sòl i la fragmentació dels hàbitats, les invasions biològiques o l'augment de concentració de CO_2 a l'atmosfera (Vitousek et al., 1997; Steffen et al., 2004). Per tant, és conseqüència d'un conjunt de factors, sovint amb interaccions entre ells, que actuen modificant les condicions del medi que predominaven fins fa unes quantes dècades. Tant la magnitud com la taxa d'aquests canvis ocorreguts en els darrers 150 anys, no tenen precedents en el darrer mig milió d'anys, fet que explica la dificultat o impossibilitat per moltes espècies per adaptar-s'hi.

L'estudi del canvi global ha crescut de forma exponencial en les darreres quatre dècades, des d'una perspectiva obligadament multidisciplinària que inclou meteoròlegs, químics, biòlegs, economistes, etc. (Steffen et al., 2004). La recerca ha anat dirigida en primer lloc a confirmar l'existència i quantificar la magnitud i velocitat d'aquests canvis, i també a estudiar com mitigar els impactes derivats i com adaptar-s'hi, passant per la identificació i avaluació dels impactes concrets que està produint el canvi global sobre els organismes, ecosistemes i els cicles biogeoquímics. Per exemple, en el cas del canvi climàtic i dels ocells, s'ha vist que pot provocar canvis fenològics (canvi en l'època de nidificació i/o migració), efectes sobre la reproducció (mida dels ous, èxit reproductor, etc.), canvis en la mida de població, desajustos entre els recursos tròfics i el cicle vital, etc. (Sanz et al., 2003; Crick, 2004; Both et al., 2006; Carey, 2009). Més enllà d'aquests impactes concrets, però, el canvi global és el principal motor de la pèrdua de biodiversitat (Vitousek et al., 1997; Brook et al., 2008).

La pèrdua de biodiversitat és un terme molt actual, malauradament, que es refereix al procés pel qual es van extingint o perdent espècies, poblacions i variabilitat genètica a una velocitat anormalment alta. Al llarg de la història de la vida, sempre hi ha hagut pèrdua d'espècies, a la vegada que n'apareixien de noves, però actualment la pèrdua de biodiversitat es produeix a un ritme molt elevat, que ha portat força autors a parlar de la sisena gran extinció (May et al., 1995). Per exemple, es coneix que s'han extingit una quarta part de les espècies d'ocells en els darrers 2000 anys (Vitousek et al., 1997), malgrat que aquesta és una finestra temporal més àmplia de la que s'acostuma a parlar quan es fa referència a la pèrdua de biodiversitat. En els darrers 500 milions d'anys, es coneixen cinc grans períodes amb elevades taxes d'extinció d'espècies, causades per motius geològics, climàtics, etc. Però la novetat de l'actual pèrdua de biodiversitat o sisena extinció, és que l'home n'és el principal causant. L'activitat humana i el creixement de la població mundial, especialment a partir de la revolució industrial, han provocat una transformació radical dels ecosistemes que la majoria d'espècies i hàbitats no són capaços d'afrontar, és a dir d'adaptar-s'hi.

La pèrdua de biodiversitat en els ambients agrícoles

Els ambients agrícoles són fruit d'una modificació del paisatge que l'home ha anat forjant poc a poc, des del Neolític, quan va aprendre a cultivar per tal d'obtenir aliment per ell o pel bestiar (Blondel & Aronson 1999). Tot i el seu origen antròpic, han mantingut fins avui en dia comunitats molt riques amb una alta diversitat, i avui en dia es consideren uns hàbitats importants per la conservació de moltes espècies, com en el cas dels ocells (Tucker & Heath 1994; Pain & Pienkowski, 1997). De fet els ambients agrícoles ocupen el 50% de la superfície d'Europa (Tucker & Heath, 1994) i per tant allotgen nombroses espècies, algunes de les quals, actualment depenen exclusivament d'aquests ambients d'origen antròpic (Pain & Pienkowski, 1997).

Els ambients agrícoles no s'han vist exclosos del canvi global i, com tots els ambients del planeta, han estat profundament modificats en les darrers dècades (Blaxter & Robertson 1995). De fet, el canvi i la transformació d'usos és un dels agents del canvi global més impactant sobre la biodiversitat, més fins i tot que el canvi climàtic (Vitousek et al., 1997). A partir dels anys 50 del segle XX, arrel de la revolució agrícola, els ambients agrícoles han començat a veure's seriosament modificats i s'ha començat a detectar una pèrdua de biodiversitat molt rellevant en diferents grups taxonòmics (Benton et al., 2003). La millora tecnològica (maquinària agrícola, cultius genèticament modificats, pesticides, etc.) ha permès un ràpid creixement de la producció agrícola, primer a Europa i Nord-Amèrica i, posteriorment, a altres zones del planeta, que ha resultat en una ràpida intensificació agrícola mai vista fins ara. El resultat d'aquesta intensificació ha estat la homogeneïtzació i simplificació del paisatge i de les comunitats d'espècies que l'ocupen (Chamberlain et al., 2000; Benton et al., 2003). El procés d'intensificació agrària inclou diversos processos, com ara la pèrdua de taques de vegetació natural o semi-natural entre parcel·les agrícoles, la introducció de regadiu, el drenatge de terres, l'eliminació de marges entre camps per crear parcel·les més grans (concentració parcel·lària), una major intensitat i freqüència de llaurat dels camps, l'increment en l'ús d'adobs, l'aplicació de pesticides, l'augment de superfície en monocultiu, la reducció de les rotacions de cultius, etc. (Krebbs et al., 1999; Chamberlain et al., 2000).

Actualment està comprovat l'impacte que aquesta intensificació agrícola ha tingut sobre la biodiversitat (Flowerdew, 1997; Sotherton & Self, 2000) i en particular sobre els ocells, un dels grups més estudiats (Fuller at al., 1995; Siriwardena et al., 1998a; Chamberlain et al., 2000; Donald et al., 2001). Per exemple, Fuller et al. (1995), van trobar que entre 1970 i 1990 el 86% dels ocells dels medis agrícoles del Regne Unit havien vist com la seva àrea de distribució s'havia reduït i el 83% havien sofert un descens poblacional. Per altra banda, Donald et al. (2001) van comprovar com un indicador de la intensificació agrícola com és la producció de cereal per unitat de superfície, per ella sola, explicava el 30% dels canvis poblacionals dels ocells agrícoles a Europa, tot i que detectaven una major intensificació a Europa occidental que a Europa de l'Est (sobretot a partir de 1980) i, conseqüentment, un major impacte sobre les tendències poblacionals en els països de la UE. Els mecanismes proposats pels quals aquesta intensificació ha afectat negativament les poblacions d'ocells són diversos, però es poden resumir en una reducció de l'aliment disponible (llavors i insectes) (Campbell et al., 1997; Brickle et al., 2000; Boatman et al., 2004; Hart et al., 2006), menys hàbitat adequat per a la nidificació i alimentació (Chamberlain et al., 1999; Fuller et al., 2004; Gillings et al., 2005) o mortalitat directa causada per maquinària o similars (Crick et al., 1994; Corbacho et al., 1999). Al seu torn, la disminució de la quantitat i/o qualitat de recursos derivada de la intensificació agrícola, ja siguin de tipus tròfic com d'hàbitat, etc., pot tenir el seu impacte sobre els paràmetres demogràfics principals que, al final, són els que determinaran la tendència poblacional, un canvi en l'àrea de distribució o fins i tot un canvi en el risc d'extinció d'una espècie o població. En el cas dels ocells en els medis agrícoles, per exemple, s'ha comprovat com la intensificació agrícola ha afectat la dinàmica poblacional d'espècies a través d'un canvi en la supervivència anual dels exemplars (Siriwardena et al., 1998b), o a través dels paràmetres reproductius (Brickle et al., 2000; Siriwardena et al., 2000).

Biologia de la conservació i risc d'extinció

A finals dels anys 70 i principis dels anys 80 dels segle XX, neix la disciplina de la biologia de la conservació, com a conseqüència de la creixent sensibilització de la societat envers un problema que cada vegada es feia més evident, el creixent impacte humà sobre el planeta, en forma de pol·lució, degradació i sobreexplotació dels hàbitats, extinció d'espècies, etc. La biologia de la conservació s'ocupa d'estudiar la natura i la biodiversitat amb l'objectiu de protegir espècies, hàbitats i ecosistemes front a la degradació i simplificació de les relacions biòtiques i, també, lògicament, front a una excessiva taxa d'extinció (Soulé, 1985). En definitiva, és la disciplina que té per objectiu principal aturar o contrarestar la pèrdua de biodiversitat i minimitzar la probabilitat d'extinció d'espècies amenaçades.

Ja als inicis de la disciplina de la biologia de la conservació, es van definir dos grans paradigmes o contextos sota els quals es pot estudiar el destí i els processos que regeixen una població de qualsevol espècie: el paradigma de la població de "mida petita" i el de la població "en declivi" (Caughley, 1994). El primer es centra en espècies o poblacions molt amenaçades, amb una alta probabilitat d'extinció a través de factors atzarosos o d'estocasticitat, degut a la seva petita mida. Es tracta d'una aproximació a la biologia de la conservació que tracta d'evitar l'extinció d'una espècie o la pèrdua de diversitat genètica, a partir de l'increment de la mida de la població, ja que aquesta és la principal causa d'extinció quan una població arriba a valors molt baixos. Caughley (1994) diu que es tracta de curar un malalt, sovint amb urgència, i per això fa èmfasi en el segon paradigma, el de la població "en declivi" que treballa sobre poblacions en regressió, però que encara mantenen poblacions grans, amenaçades per factors deterministes que cal identificar primer i resoldre després, a través de la gestió i conservació. Així doncs, els dos paradigmes posen en evidència que les principals forces que porten al declivi (deterministes) no tenen perquè ser les mateixes o no tenen perquè actuar amb la mateixa intensitat que les que, finalment, acaben causant l'extinció d'una població o espècie (forces estocàstiques) que ja ha arribat a una situació límit, amb un nombre reduït d'exemplars. Algun autor ha criticat aquesta distinció tan nítida entre els dos paradigmes, ja que en general, aquests factors actuen de forma simultània i, per tant, els dos paradigmes són sovint necessaris de cara a evitar l'extinció d'espècies amenaçades (Hedrick et al., 1996).

Quan una població mostra un tendència negativa la mida de la població disminueix i l'àrea de distribució sovint també i, per tant, inevitablement el risc d'extinció s'incrementa (Hanski, 1999; Purvis et al., 2000). A més a més, una població situada a l'àrea perifèrica de l'àrea de distribució també tendeix a tenir un estat de conservació més desfavorable, pel fet que acostuma a estar més aïllada geogràficament (i per tant, té menys possibilitat de rebre immigració) que una població central, i a tenir unes condicions ambientals menys afins als requeriments mitjans de l'espècie (Lesica & Allendorf, 1995). Per altra banda, hi ha altres factors de risc que fan algunes espècies més o menys vulnerables al risc d'extinció, com els relacionats amb la història vital (espècies amb baixa natalitat i llarga longevitat, etc.), amb el grau d'especialització (tròfica, etc.), necessitats d'espai per completar el cicle vital (territoris grans vs. territoris petits), etc. (Owens & Benett, 2000; Purvis et al., 2000; Norris 2004). Però en última instància, l'estat de conservació d'una població concreta ve determinat pels seus paràmetres demogràfics, els quals es poden resumir en la suma de naixements (natalitat) i defuncions (mortalitat), juntament amb els processos de dispersió (emigració i immigració) (Hanski, 1999; Morris & Doak, 2002). Per tant, en biologia de la conservació, a més a més de preguntar-se quines són les necessitats (requeriments ecològics i història evolutiva) i de quantificar els recursos disponibles (aliment, hàbitat, etc.) que poden estar limitant una espècie o població, en paral·lel, és recomanable endinsar-se en la dinàmica de poblacions per a identificar els paràmetres demogràfics o els processos que, en última instància, estan limitant la taxa de creixement i, en definitiva, incrementant el risc d'extinció.

A més a més de les quatre variables esmentades anteriorment (natalitat, mortalitat, emigració i immigració), hi ha altres processos a tenir en compte a l'hora de valorar el risc d'extinció d'una població (Morris & Doak, 2002): en primer lloc es produeixen fluctuacions atzaroses en els factors biòtics i abiòtics que donen lloc a l'estocasticitat ambiental i que, per definició, afecta tota la població per igual en un moment determinat (amb els seus casos extrems com són les catàstrofes). Curiosament, aquestes fluctuacions ambientals a vegades produeixen una sincronia espacial en l'abundància de poblacions separades geogràficament, però sotmeses a factors semblants (Liebhold et al., 2004). Quan diferents poblacions estan sincronitzades i són petites, el risc d'extinció encara s'incrementa més ja que els anys en que disminueix l'abundància, ho fa a tot arreu, produint un efecte acumulatiu pel global de tota la població. Una altra font de variabilitat que incrementa el risc d'extinció de poblacions petites, és l'estocasticitat demogràfica (Caughley, 1994), que representa una fluctuació atzarosa en l'eficàcia biològica (fitness) dels individus. Aquesta fluctuació, si la població és petita, pot donar lloc a situacions d'alt risc (fins i tot l'extinció directa), com per exemple que, per pur atzar, en un any determinat morin molts més mascles que femelles, dificultant la formació de parelles reproductores. En darrer lloc, tindríem l'estocasticitat genètica, que de nou afecta especialment les poblacions petites i que produeix una pèrdua de variabilitat genètica, sobretot a través de la deriva genètica o l'endogàmia (Amos & Harwood, 1998; Lande 2002), fins al punt de reduir les aptituds i les capacitats dels individus per completar el seus cicles vitals (reducció de la fertilitat, reducció de la supervivència, etc.) o adaptar-se als canvis. Avui en dia existeixen diferents tècniques moleculars que, a partir de l'anàlisi del DNA mitocondrial o nuclear, permeten estimar el grau de diversitat genètica i els possibles canvis temporals ocorreguts en el material genètic, com a conseqüència de la dinàmica poblacional (Frankham et al., 2002), així com identificar la possible existència de diferents unitats de gestió i "unitats evolutives significatives" (ESU) que poden tenir interès des del punt de vista adaptatiu i de la conservació (Moritz, 1994; Crandall et al., 2000).

A l'hora de prendre decisions sobre com gestionar una espècie o població amenaçada amb l'objectiu de revertir una tendència poblacional negativa o una disminució de l'àrea de distribució, es requereix, per tant, del màxim d'informació possible, tant de les causes com dels mecanismes que han derivat en aquest estat de conservació desfavorable (Beissinger & Dale, 2002; Norris, 2004). Cal conèixer les causes, com ara una reducció de la disponibilitat d'aliment o la pèrdua d'hàbitat, per tal d'identificar el tipus de problema (aliment, depredació, manca de llocs per nidificar, etc.) i on i quan té lloc (àrea de nidificació, època reproductora, etc.). Les causes també ens identifiquen quines mesures de conservació caldrà implementar (millora o creació de nou hàbitat, millora de les poblacions presa, etc.). Pel que fa als mecanismes demogràfics, és a dir quins paràmetres vitals s'estan veient afectats per una manca d'un recurs determinat, és important conèixer-los perquè ens permetran quantificar i comparar l'impacte sobre la taxa de creixement que tenen aquells recursos que hem identificat com a limitants (Beissinger & Dale, 2002; Morris & Doak, 2002; Naujokaitis-Lewis et al., 2008). Per tant, el coneixement dels mecanismes demogràfics pels quals un problema en el medi impacta sobre una població, ens permetrà establir un ordre d'importància i de prioritats (i ser més eficients) a l'hora de prendre decisions sobre la gestió i conservació de l'espècie o població objectiu. En aquest sentit, en els darrers anys han anat guanyant importància els anàlisis de viabilitat poblacional, com una eina molt útil per avaluar el risc d'extinció d'una o un conjunt de poblacions, i també per identificar i prioritzar els factors demogràfics clau per la seva viabilitat i als quals, possiblement, caldrà donar preferència des del punt de vista de la gestió i conservació (Purvis et al., 2000; Morris & Doak, 2002; Naujokaitis-Lewis et al., 2008).

La trenca (*Lanius minor*)

Molta de la informació bibliogràfica sobre la trenca prové, en primer lloc, de dues monografies sobre la família dels lànids, així com d'atles i altres obres genèriques o divulgatives sobre els ocells o sobre la fauna d'alguns països. En segon lloc, pel que fa a la bibliografia de caire científic (articles científics), tota la informació prové exclusivament de l'àrea d'hivernada, així com de l'àrea de nidificació de França i de la d'una població d'Europa de l'Est situada a Eslovàquia, que ha estat intensament estudiada. A partir d'aquesta tesi també s'ha generat bibliografia científica sobre la població catalana i espanyola i, més recentment, també ha aparegut alguna publicació sobre les poblacions italianes. Finalment, dir que també existeix bibliografia provinent de Rússia (sobretot històrica), difícil de localitzar i d'entendre a causa de l'idioma.

Sistemàtica i morfologia

La trenca (*Lanius minor*) és una espècie d'ocell de l'ordre dels passeriformes que pertany a la família *Laniidae*, grup format per una trentena d'espècies. La majoria dels components de la família pertanyen al gènere *Lanius* (23 espècies), els quals es distribueixen per tot el planeta, excepte Oceania (Lefranc & Worfolk, 1997). La trenca és una de les 6 espècies de lànids que podem trobar a Europa, dues de les quals són sedentàries (*Lanius meridionalis* i *Lanius excubitor*) i la resta migradores (*Lanius nubicus*, *Lanius senator*, *Lanius collurio* i *Lanius minor*). Alguns autors (Vaurie, 1955; Clancey, 1980) consideren l'existència de dues subespècies, una d'europea (*L. minor minor*) i una d'asiàtica (*L. minor turanicus*), en base a lleugeres diferències de coloració. Malgrat això, la majoria d'autors tracten l'espècie com a monotípica (veure la revisió de Lefranc & Worfolk, 1997).

En llatí, *Lanius* significa carnisser i fa referència a l'hàbit que tenen la majoria d'espècies del gènere, d'empalar les seves preses per tal d'estripar-les i trencar-les en trossets més fàcils de manipular i de ingerir (Lefranc & Worfolk, 1997). Concretament la trenca, però, és una de les espècies que té poc desenvolupat aquest comportament (Valera et al., 2001).

La trenca té una mida d'uns 20 cm de longitud, de coloració grisa a la part superior del cos, amb tons rosats al pit i ventre i negre a la part central de la cua, ales i màscara facial (Figura 1). La gorja i les plomes externes de la cua són blanques i té una distintiva franja blanca a l'ala en sentit longitudinal, que quan vola és ben visible. Com la resta de la família, té un bec (negre) ben robust i en forma de ganxo, amb el qual és capaç de trencar els exosquelets dels insectes dels quals principalment s'alimenta (Lefranc & Worfolk, 1997). Existeix poc dimorfisme sexual en aquesta espècie, tot i que els mascles tenen el front negre una mica més extens, i més blanc a la cua, trets que sovint no són fàcils d'apreciar a una certa distància (Lefranc & Worfolk, 1997; Kristín et al., 2007a).

Figura 1: Mascle de trenca (*Lanius minor*)

Distribució històrica i actual i efectius poblacionals

La trenca té una distribució paleàrtica que abasta des de la península ibèrica fins a les estepes de Kazakhstan, en sentit longitudinal, i des de la riba nord del mar Mediterrani fins a la plana russa (paral·lel 55º), en sentit latitudinal (Lefranc & Worfolk, 1997). Dins d'aquest ampli rang de distribució, però, es restringeix a les àrees més planes i càlides, sempre amb clima mediterrani o continental. L'àrea d'hivernada es situa al sud d'Àfrica, concretament al Kalahari i l'àrea perifèrica, incloent el sud d'Angola, Namíbia, Botswana, nord de Sud-àfrica i part de Moçambic (Herremans, 1998a). Cal destacar que l'àrea d'hivernada és cinc vegades més petita que l'àrea de reproducció (Lefranc & Worfolk, 1997).

Durant el segle XIX va ser una au comú a Europa occidental, començant a reduir la seva àrea de distribució a partir dels inicis del segle XX, desapareixent d'Alemanya, Bèlgica, Luxemburg, Suïssa i gran part de França (Lefranc & Worfolk, 1997) (Figura 2). La única cita del segle XIX a Espanya és de Vayreda (1883), qui esmenta que no és una espècie comuna, però que nidifica en diverses localitats a la província de Girona. No és fins l'any 1947 que es torna a citar l'espècie, en aquest cas a la província de Lleida (Maluquer-Sostres, 1952). Després de la reducció de l'àrea de distribució constatada al llarg del segle XX a Europa occidental (Lefranc, 1995), a principis de segle actual, ja només quedava un rosari de petites poblacions aïllades a la zona mediterrània: 3 poblacions a Espanya (Lleida, Girona i Aragó) que sumaven menys de

30 parelles en total (Giralt & Bota, 2003; Giralt et al., 2010) i 2 poblacions a França (Aude i Montpeller) (Bara, 1995; Isenmann et al., 2000) amb unes 40 parelles en conjunt (Figura 3). La distància entre aquestes poblacions oscil.la entre els 35 i 220 km. També resten actualment unes quantes poblacions a Itàlia (Figura 2), sense que se'n conegui amb detall ni la distribució exacta ni el nombre d'efectius (1.000-2.500 parelles)(BirdLife International, 2004). La distribució és molt més continua a Europa de l'Est, essent Romania i Bulgària els països que alberguen gran part de la població europea actual, estimada en un màxim de 320.000 parelles per tot el continent (BirdLife International, 2004; Kristín, 2008). La població mundial es va estimar, a mitjans dels anys 90, en 5.000.000-7.000.000 d'individus a l'àrea d'hivernada (Herremans, 1998a). Hi ha poca informació sobre la situació de les poblacions asiàtiques, on encara és un ocell comú (Kristín, 2008).

Figura 2: Distribució històrica i fins a principis del segle XXI de la trenca (*Lanius minor*) a l'època reproductora (hemisferi nord) i durant l'hivernada (hemisferi sud), i ruta migratòria pre-nupcial i post-nupcial (Font: Lefranc & Worfolk, 1997).

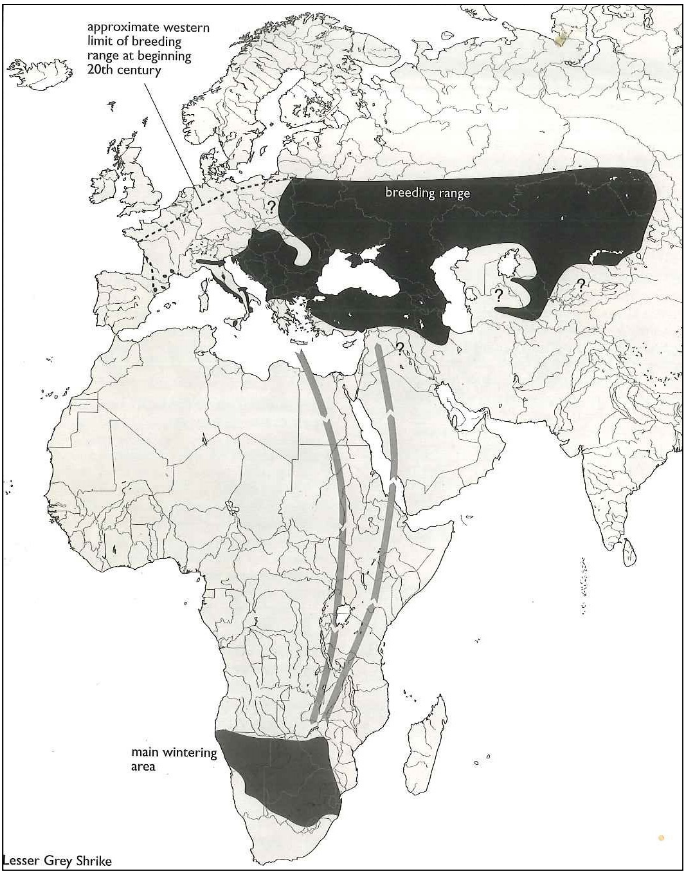
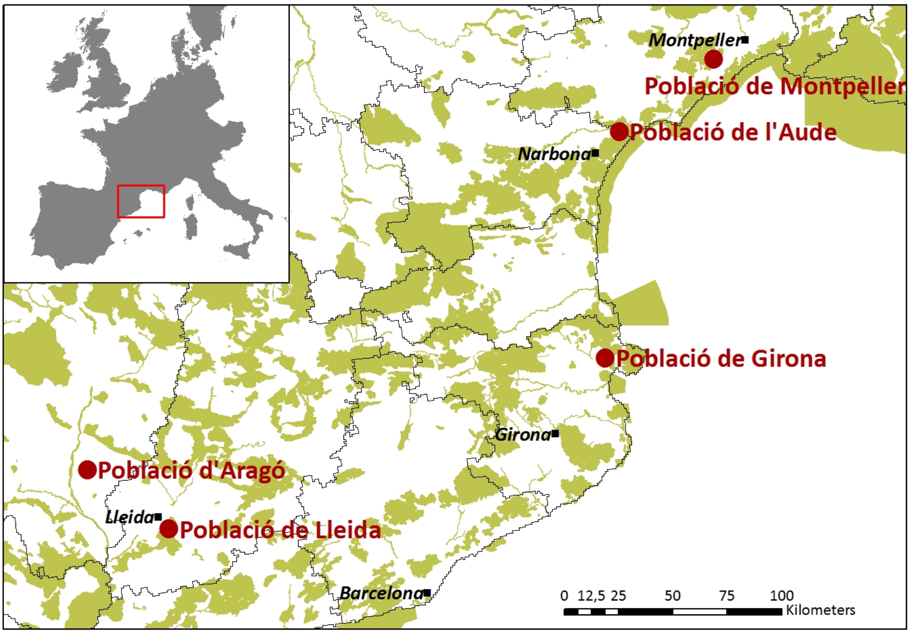


Figura 3: Distribució de les poblacions més occidentals de trenca a principis del segle XXI. La població de Girona es va extingir l'any 2002 i la població d'Aragó al 2010. En verd es mostra la Xarxa Natura 2000.



Migració

Es tracta d'un migrador de llarga distància, que realitza un dels recorreguts més llargs entre els passeriformes, ja que les àrees de reproducció i d'hivernada se situen a uns 10.000 km de distància. Totes les poblacions migren per un estret rang longitudinal de l'est d'Àfrica (Tanzània i Uganda) i, més al nord, entre Grècia i l'Iran. Això implica que les poblacions més occidentals com la catalana, abandonen les àrea de cria primer en direcció nord-est i immediatament després en direcció est fins arribar a Grècia, i és llavors quan creuen el mar Mediterrani en el seu camí cap a Àfrica. Les poblacions europees realitzen una migració en llaç, sent el trajecte pre-nupcial més oriental que el post-nupcial. Aquest tipus de migració en llaç pot estar reflectint una possible expansió històrica de l'espècie (Rüegg & Smith, 2002), possiblement des del Pròxim Orient cap a Europa.

Hàbitat i dieta

L'hàbitat originari de la trenca està lligat a sabanes obertes, semi-deserts i grans àrees estepàries (Lefranc, 1993; Lefranc & Worfolk, 1997). La progressiva expansió de l'agricultura i la conseqüent reducció de les àrees forestals li deuria permetre colonitzar Europa, adaptant-se a les zones agrícoles conreades de forma no intensiva. Tolera les zones agrícoles de regadiu sempre i quan no estiguin gestionades de forma intensiva, és a dir que mantinguin certes característiques com la presència d'arbres aïllats i, sobretot, de força marges entre les parcel·les. En ambients agrícoles, ocupa zones dominades per cultius herbacis, com mosaics de cereals, guarets, pastures, prats, horts i també en zones de vinya (Figura 4) (Kristín, 1995; Isenmann & Debout, 2000; Wirtitsch et al., 2001). A una de les poblacions franceses, Isenmann et al. (2000) van observar que més del 70% dels intents de cacera es feien en guarets o camps abandonats i, a Eslovàquia, Kristín (1995) indica que la majoria de preses eren obtingudes en prats i pastures, sense arribar a quantificar-les. Tot i ser un especialista de zones agrícoles i estepàries, requereix la presència d'alguns arbres (aïllats o formant fileres) per fer-hi el niu, preferentment en arbres de port rellevant i generalment de més de 5m d'altura, amb capçades àmplies i brancatge frondós (Figura 4) (Lefranc & Worfolk, 1997).

Caça en zones de vegetació herbàcia (cultius, horts, pastures, etc.) i també arbustiva, sempre amb un cert percentatge de sòl nu que faciliti l'accés als insectes (Figura 4) (Lefranc & Worfolk, 1997; Wirtitsch et al., 2001). Per poder caçar, també és important la presència de posadors (marges entre cultius, tanques, arbusts, etc.) que facilitin l'accés a les preses (Lefranc & Worfolk, 1997). Es tracta d'un caçador "sit & wait" (Beachly et al., 1995), és a dir necessita punts elevats (marges, arbres, petits arbusts, fils elèctrics, etc.) des d'on localitza les seves preses, que captura principalment al terra, però també en vol (Kristín, 1995; Isenmann et al., 2000). La dieta està formada, quasi exclusivament, per insectes, i molt especialment coleòpters i ortòpters, que acostumen a constituir més del 50% de la dieta, motiu pel qual es pot considerar un especialista a nivell tròfic, tot i que també pot alimentar-se d'himenòpters, aràcnids i d'algun petit micromamífer (Kristín, 1995; Lepley et al., 2004). També se la pot considerar especialista tròfica en el sentit que selecciona insectes de mida mitjana i gran (>20 mm de longitud mitjana) (Kristín, 1995; Lepley et al., 2004), que justament acostumen a ser menys abundants que els insectes de mida més petita. Pot aprofitar recursos temporalment molt abundants, com són les explosions de formigues voladores o de determinats escarabats (Hoi et al., 2004). Rarament empala les seves preses, a diferència d'altres lànids (Valera et al., 2001).

Figura 4: Territori de trenca on s'observa l'hàbitat de nidificació (filera d'arbres a l'esquerra) i la zona d'alimentació (camps i marges a la dreta)(Foto: Juan Bécares)

Reproducció

És una espècie monògama i territorial, que pot i acostuma a nidificar en agregacions, de forma semi-colonial, havent-se trobat de forma excepcional dues parelles nidificant al mateix arbre (Lefranc & Worfolk, 1997). Els territoris poden tenir des 2.9 fins a 14 ha (Kristín, 2008). Realitza un sola posta (generalment 5-7 ous), que s'inicia al mes de maig, tot i que en cas de fracassar, pot realitzar més d'una posta de reposició. La incubació la realitza només la femella i dura uns 14-16 dies. El mascle s'ocupa de caçar per a la femella i també per als polls mentre aquests tenen menys d'una setmana d'edat, moment en què la femella comença a col·laborar en l'obtenció de l'aliment. Els polls resten al niu per un període de 14-18 dies i, posteriorment, depenen dels pares durant unes 3 setmanes més, aproximadament.

Causes de la regressió i factors limitants

Les causes del declivi històric i actual de l'espècie a Europa, s'han atribuït principalment a dos factors, ambdós causats per la intsensificació agrícola. En primer lloc es fa referència a la pèrdua i fragmentació de l'hàbitat, degut a canvis d'usos agrícoles, expansió de monocultius i regadius intensius, eliminació de marges des d'on caçar i arbres necessaris per a nidificar, etc. (Lefranc, 1993; Tucker & Heath, 1994). En segon lloc, es menciona la disminució de les poblacions d'insectes, a causa de l'ús excessiu de plaguicides i també per la simplificació del paisatge agrícola. En aquest sentit, la majoria de treballs destaquen l’evident transformació en els medis agrícoles succeïda a Europa occidental i en particular en les zones de nidificació d’aquesta espècie (Lefranc, 1993; Isenmann et al., 2000) en contrast amb la situació a Europa de l’Est, on encara es manté una agricultura força extensiva, és a dir sense un ús generalitzat de plaguicides i mantenint els mosaics agrícoles (Kristín, 1995; Wirtitsch et al., 2001). No obstant, no hi ha estudis específics que, per exemple, correlacionin a nivell temporal la degradació de l’hàbitat amb la pèrdua de territoris d’una població determinada, i només un treball que compari en una mateixa zona, els diferents tipus d’hàbitat en relació al resultat reproductiu, en aquest cas sense trobar cap efecte (Wirtitsch et al., 2001). Tampoc s’han pogut realitzar estudis experimentals que avaluïn l’efecte de l’hàbitat o de la disponibilitat d’aliment en relació als paràmetres reproductius, malgrat que Hoi et al., (2004) sí que van comprovar que els anys amb explosions demogràfiques d’una espècie d’escarabat de mida mitjana o gran, es traduïen en un major pes corporal dels joves, fet que podria tenir implicacions per a la seva posterior supervivència. Així mateix, Lepley et al. (2004) comproven que en una de les poblacions franceses, la dieta difereix entre les parelles que nidifiquen de forma aïllada i les que ho fan de forma agregada, però no observen que aquesta diferència tingui implicacions a nivell reproductiu. Per la seva banda, Kristín (1995) i Wirtitsch et al. (2001) descriuen la importància de la disponibilitat d’insectes grans i la presència d’ecotons en les seves poblacions d’Europa de l’Est com a garantia d’un bon èxit reproductor i un estat saludable de la població. En definitiva, tot i el consens general i l’existència d’algun indici que la intensificació agrícola ha estat el principal motor del declivi de l’espècie, manquen evidències nítides que lliguin alguna característica de l’hàbitat o de la disponibilitat tròfica amb algun paràmetre demogràfic.

Apart de la intensificació agrícola, s'han apuntat factors climàtics a l’Europa més atlàntica, on successius estius humits en determinats períodes del segle XX, podrien haver causat una disminució substancial de la productivitat i de l’èxit reproductor, fins al punt de contribuir a l’extinció de les poblacions més nord-occidentals (França, Bèlgica, etc.)(Lefranc, 1993). Actualment, en el context de canvi climàtic i de pujada de les temperatures, aquest factor tindria poc suport i, de fet, si aquest fos el principal factor responsable de la desaparició de l’espècie en aquella zona, s’esperaria una recolonització progressiva, encara que fos parcial, que no s’ha produït. Per contra, avui en dia, es podrien esperar problemes derivats del canvi climàtic a les àrees de cria més meriodionals, per exemple com a conseqüència de desajustos entre el pic de disponibilitat d’aliment i l’època de nidificació, com s’ha demostrat per a altres espècies d'ocells que són migradors de llarga distància i que tenen poca flexibilitat per canviar els seus calendaris de migració (Berthold ,1998; Herremans, 1998b; Both et al., 2006; Rubolini et al., 2010).

Pel que fa a la zona d'hivernada, de nou un canvi de l'hàbitat i, concretament, la subtitució de pastures per matollars, a causa de la sobre-pastura, podria ser una de les principals amenaces en aquella zona (Herremans, 1998a). Per altra banda, el mateix autor descarta que l'ús de plaguicides en aquella zona pugui ser rellevant per a l'espècie, tal i com s'havia suggertit (Lefranc, 1993), ja que la principal àrea d'hivernada no coincideix amb les zones d'aplicació d'aquests productes.

En darrer lloc, un altre factor que segons la bibliografia pot limitar les poblacions de forma més local, sense que necessàriament sigui una causa de regressió, és la depredació de nius per part garses (*Pica pica*), gats domètics (*Felis silvestris catus*), etc. (Bara, 1995; Lefranc & Worfolk, 1997; Kristín et al., 2000), malgrat que les taxes de fracàs publicades (per depredació i altres causes), en tots els casos són força inferiors al 50% i, per tant, no excessivament altes.

Les poblacions occidentals de trenca com a model d'estudi en biologia de la conservació: poblacions estudiades i període d'estudi

Els estudis dirigits a entendre les causes de regressió i a avaluar el risc d'extinció d'espècies o poblacions són bàsics en el context actual de pèrdua de biodiversitat (Purvis et al., 2000; Beissinger & Dale, 2002; Norris, 2004). Les poblacions occidentals de trenca tenen diferents característiques que les fan interessants des d'aquest punt de vista: 1) a l'inici d'aquest estudi (2001) feia més de dues dècades que tenien poblacions aparentment petites (menys de 50 parelles) i geogràficament aïllades, fet que obliga a tenir en compte aspectes deterministes i també estocàstics per entendre el seu comportament, 2) es situen a la perifèria de l'àrea de distribució global i per tant, poden estar sotmeses a condicions biòtiques i abiòtiques diferents a les de les poblacions situades al centre de l'àrea de distribució (Lesica & Allendorf, 1995; Williams et al., 2003), fins i tot amb possibles impactes a nivell genètic que les pot fer valuoses des del punt de vista adaptatiu i de la conservació, i 3) la trenca és una especialista d'ambients agrícoles, un hàbitat molt antropitzat i que ha sofert canvis molt radicals en les darreres dècades i on, per tant, fer compatibles l'activitat humana (agrícola) i la conservació esdevé un gran repte, si es vol frenar la pèrdua de biodiversitat actual.

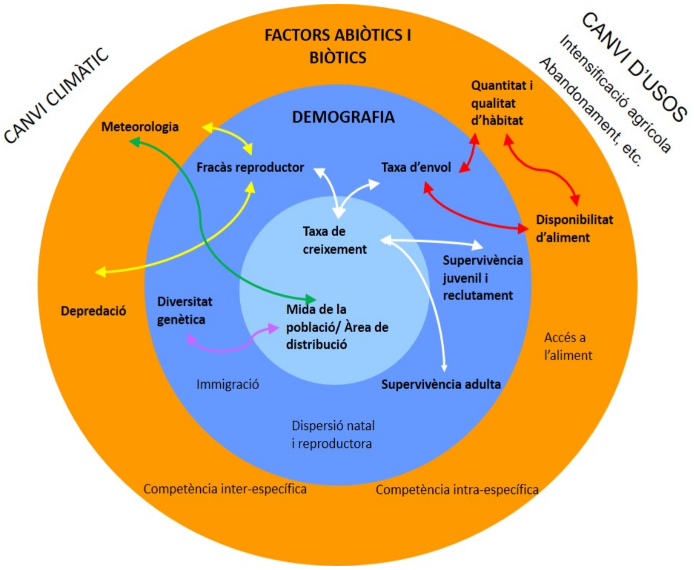
Aquesta tesi s'ha centrat sobretot en l'estudi de la població espanyola més gran (Lleida), però també inclou dades de totes les altres poblacions més occidentals: dos capítols inclouen dades de Girona, un capítol inclou dades d'Aragó i un altre capítol inclou informació de les dues poblacions franceses. Finalment, en un parell de capítols també es mostren i s'analitzen dades de la població eslovaca (Europa de l'Est).

Pel que fa al període d'estudi d'aquesta tesi, la majoria de la informació utilitzada per a la seva elaboració fa referència al període 2001-2006, malgrat que vaig començar a recollir dades sobre aquesta espècie l'any 1998 (cas de Girona) i que el seguiment de les dues poblacions catalanes es va allargar fins l'any 2010. Hi ha dues excepcions, ja que en un capítol de la tesi s'utilitzen dades anteriors (des de 1989) al període 2001-2006, cedides pels seus autors, i en un altre capítol s'utilitzen dades posteriors a 2006. En el període d'estudi més estricte (2001-2006) la població va passar de 18 parelles (4 a Girona i 14 a Lleida (però 19 al 2002 només a Lleida)) fins a 10 parelles (totes a Lleida). L'any 2010, quan vaig finalitzar el seguiment de l'espècie, només quedava 1 parella a Lleida, s'acabava d'extingir la població d'Aragó i la de Girona ho havia fet l'any 2002. Pel que fa a les poblacions franceses, contaven amb 47 parelles l'any 2001 i amb 17 parelles l'any 2010. En el moment de la presentació d'aquesta tesi (2015), les poblacions franceses estan en una situació similar a l'any 2010 i la població de Lleida s'ha mantingut (2 parelles el 2015), en el darrer cas degut a l'existència d'un programa de cria en captivitat (veure discussió, apartat de implicacions per a la gestió).

OBJECTIUS

L'objectiu general d'aquesta tesi és descriure el declivi en els darrers 10-20 anys de les poblacions més occidentals i perifèriques de trenca a Europa (Catalunya, Espanya i França), i identificar les causes de regressió, així com els mecanismes i paràmetres demogràfics que tenen un paper més rellevant en el risc d'extinció d'aquestes poblacions (Figura 5). L'objectiu últim del treball també és donar propostes concretes per a la conservació i gestió d'aquestes poblacions, així com orientar sobre la seva prioritat i idoneïtat.

Figura 5: Marc conceptual en que s'engloba la present tesi: de fora endins, es mostren, en primer lloc, dos dels principals factors de canvi global, a continuació els factors biòtics i abiòtics que conformen les condicions ambientals d'una població o espècie, les quals acaben determinant els valors dels paràmetres demogràfics que dirigeixen la dinàmica i viabilitat d'una població. Tot plegat defineix l'estat de conservació d'una espècie, que es pot sintetitzar en la taxa de creixement, mida de la població i àrea de distribució. Les fletxes mostren els factors i paràmetres estudiats a la present tesi i cada color de fletxa representa un capítol diferent (Capítol 1: fletxa verda; Capítol 2: fletxa groga; Capítol 3: fletxa vermella; Capítol 4: fletxa lila; Capítol 5: fletxa blanca):



Els objectius específics a partir dels quals s'estructuren els diferents capítols de la present tesi són els següents:

Capítol 1: En primer lloc, l'objectiu és certificar i quantificar el declivi i la reducció de l'àrea de distribució de les poblacions occidentals des dels anys noranta fins a principis del segle XXI. En segon lloc, veure si les poblacions estan governades pels mateixos factors i en aquest cas esperaríem observar una sincronia espacial entre elles, per exemple en els seus efectius poblacionals. Donat que la meteorologia s'ha citat com una possible causa de regressió de l'espècie (Lefranc & Worfolk, 1997) i que el mateix factor sovint pot provocar sincronia espacial entre poblacions (Liebhold et al., 2004), en aquest treball s'avalua si les fluctuacions interanuals en l'abundància de tres poblacions responen a factors climàtics i al grau de desenvolupament de la vegetació (NDVI). També s'analitza si existeixen tendències climàtiques a les àrees de nidificació i d'hivernada que puguin contribuir a la regressió de les poblacions més occidentals de l'espècie.

Capítol 2: Si tal i com menciona la bibliografia (Lefranc & Worfolk, 1997; Kristín, 2008), la major part d'amenaces per aquesta espècie es produeixen a l'àrea de nidificació, és convenient realitzar algun estudi comparatiu entre poblacions nidificants en diferents estats de conservació. L'objectiu d'aquest treball és **c**omparar els paràmetres reproductors entre una població situada a la perifèria (Lleida) i una població situada a la zona més propera al centre de l'àrea de distribució (Eslovàquia), per tal de detectar diferències i identificar algun paràmetre vital o mecanisme responsable del diferent estat de conservació entre les dues poblacions (declivi a la perifèria i estabilitat a la població central). També s'analitza el grau de gregarisme de la trenca i l'abundància d'un depredador de nius a la població perifèrica en relació a les taxes reproductives, per tal d'extreure possibles conclusions de gestió per les àrees de nidificació.

Capítol 3: La pèrdua d'hàbitat i la manca de recursos tròfics (insectes) degudes a la intensificació agrícola a Europa occidental, s'han postulat com la principal causa de regressió de moltes espècies agrícoles i, en particular, de la trenca. Per això, en aquest capítol volem comprovar si hi ha variabilitat entre hàbitats en la disponibilitat tròfica i si, com seria d'esperar, aquest és un aspecte clau en la selecció de l'hàbitat de cacera i en el resultat de la reproducció de les parelles (taxa d'envol de polls). L'objectiu final és oferir eines per a una millor gestió de l'hàbitat a les àrees de nidificació, i evidenciar, per primer cop en aquesta espècie, si la intensificació agrícola pot haver influït en les poblacions a nivell demogràfic, a través de la pèrdua d'hàbitat o la disminució de les poblacions d'insectes.

Capítol 4: A la perifèria de l'àrea de distribució d'una espècie, les poblacions sovint són més petites i es troben aïllades, fet que pot comportar una pèrdua de diversitat genètica provocada per l'endogàmia o la deriva genètica (Amos & Harwood, 1998). Aquest aspecte és rellevant des del punt de vista de la conservació, ja que pot reduir la capacitat dels individus per fer front a les condicions ambientals existents o a futurs canvis i, per tant, la seva eficàcia biològica. L'objectiu del present treball és avaluar la diversitat genètica de diferents poblacions europees i asiàtiques a través de marcadors mitocondrials i nuclears, i determinar si el declivi històric de les poblacions occidentals ha tingut efectes genètics que puguin afectar la seva viabilitat futura. Aquest treball també vol explorar la possible existència d'una estructura genètica entre diferents poblacions i, concretament, si es poden definir diferents unitats de gestió a nivell genètic amb interès evolutiu i de conservació (Moritz, 1994; Crandall et al., 2000) o, fins i tot si es poden identificar diferents subespècies de trenca, tal i com han suggerit alguns autors (Vaurie, 1955; Clancey, 1980).

Capítol 5: Per conèixer les possibilitats de conservació i gestió d'una població o espècie, més enllà de les causes de regressió o dels factors que n'estan limitant el creixement, és necessari obtenir una visió integrada del paper relatiu que tenen els diferents paràmetres demogràfics en el seu risc d'extinció i la seva taxa de creixement (Purvis et al., 2000; Morris & Doak, 2002). Aquest treball analitza, per primer cop en aquesta espècie, el rol de les taxes reproductives i de les taxes de retorn en el risc d'extinció i el declivi d'una població, a través d'un anàlisi de viabilitat poblacional que integra tota la informació demogràfica disponible. També es discuteix el paper de l'aïllament geogràfic i l'estocasticitat en la dinàmica d'aquesta població i de la resta de nuclis occidentals de trenca. L'objectiu final és explorar l'eficiència de les diferents possibilitats de gestió i conservació, determinant l'ordre d'importància entre els diferents paràmetres demogràfics, en base a la seva influència sobre la taxa de creixement i el risc d'extinció.

INFORME DEL DIRECTOR

El doctorando David Giralt Jonama presenta su tesis doctoral titulada "Declive del Alcaudón Chico *(Lanius minor*) en el límite occidental del área de distribución: causas, mecanismos y propuestas de conservación". El director de tesis, el Dr. Francisco Valera Hernández informa que esta tesis doctoral está formada por cinco trabajos en formato artículo, tres de los cuales ya han sido publicados en revistas científicas internacionales de prestigio, incluidas en el Science Citation Index (SCI). Los otros dos artículos están en preparación y serán enviados en breve. Ninguno de los coautores de los artículos ha utilizado ninguno de los trabajos, parcial o totalmente, en ninguna otra tesis doctoral. A continuación se detalla la contribución científica que ha realizado el doctorando en cada uno de los artículos, así como su factor de impacto (Thomson Institute for Scientific Information) en el año de publicación:

Capítulos

Giralt, D. & Valera, F., 2007. Population trends and spatial synchrony in peripheral populations of the endangered Lesser Grey Shrike in response to environmental change. Biodiversity and Conservation 16: 841-856.
Factor de impacto (2007): 1.421
El doctorando DGJ ha participado en el diseño del trabajo, en la recogida y el análisis de datos y en la redacción del artículo.

Giralt, D. & Valera, F., (en preparación). Breeding at the border of the range: comparing peripheral and central populations to understand the decline of the Lesser Grey Shrike (*Lanius minor*). Manuscrito.
El doctorando DGJ ha participado en el diseño del trabajo, en la recogida y el análisis de datos y en la redacción del artículo.

Giralt, D., Brotons, LL., Valera, F. & Kristin, A., 2008. The role of natural habitats in agricultural systems for bird conservation: the case of the Threatened Lesser Grey Shrike. Biodiversity and Conservation 17: 1.997-2.012.
Factor de impacto (2008): 1.473
El doctorando DGJ ha participado en el diseño del trabajo, en la recogida y el análisis de datos y en la redacción del artículo.

Kvist, L., Giralt, D., Valera, F., Hoi, H. Kristin, A., Darchiashvili, G., & Lovász, P., 2011. Population decline is accompanied by loss of genetic diversity in the Lesser Grey Shrike Lanius minor. Ibis, 153: 98-109.

Factor de impacto (2011): 2.430

El doctorando DGJ ha participado en el diseño del trabajo, en la recogida y análisis de datos y en la redacción del artículo.

Giralt, D., Mañosa, S, Brotons, LL. & Valera, F., (en preparación). Return rates versus reproductive rates and the viability of a small and marginal population of Lesser Grey Shrike. Manuscrito.

El doctorando DGJ ha participado en el diseño del trabajo, en la recogida y el análisis de datos y en la redacción del artículo.

Almería, 30 de septiembre de 2015

Dr. Francisco Valera Hernández
Departamento de Ecología Funcional y Evolutiva
Estación Experimental de Zonas Áridas
Consejo Superior de Investigaciones Científicas

RESULTATS I DISCUSSIÓ GENERAL

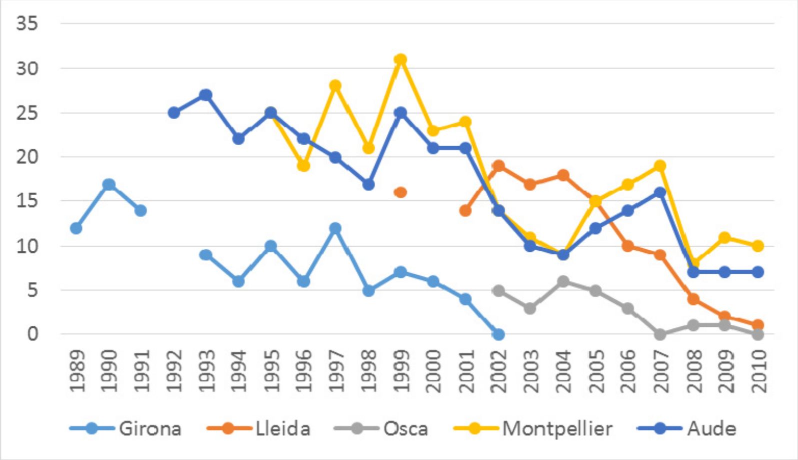
Conèixer les causes per les quals una espècie o població té un estat desfavorable de conservació és un tema central en biologia de la conservació (Caughley, 1994; Beissinger & Dale, 2002; Norris, 2004). Aquest coneixement pot permetre implementar mesures de conservació i gestió per revertir la situació desfavorable, sempre i quan es consideri oportú des de la societat. Per tant, idealment, cal un sistema de monitoratge en el temps (no necessàriament orientat a una sola espècie) que permeti detectar els possibles canvis en la tendència poblacional en l'àrea de distribució, com per exemple els programes de seguiment basats en ciència ciutadana (Bonney et al., 2009). Un cop detectat que una o un conjunt d'espècies o poblacions passen a tenir un estat de conservació desfavorable a partir d'un seguiment estàndard, caldria iniciar estudis concrets que identifiquin les causes i els mecanismes pels quals el seu estat de conservació ha passat a ser desfavorable. Malauradament, la realitat en el món de la conservació és que moltes espècies es comencen a estudiar en profunditat quan la situació és més crítica, i no només fa anys que tenen tendències negatives o desconegudes, sinó que ja s'ha reduït molt la seva àrea de distribució i/o la mida de la població, és a dir quan ja s'ha entrat en el paradigma de la població petita (Caughley, 1994; Morris & Doak, 2002).

Constatació i conseqüències del declivi de les poblacions perifèriques d'Europa occidental

Fins als anys 90, la bibliografia indicava que la trenca estava en regressió a Europa occidental, però la informació existent sobre l'estat de les poblacions era precària, tant a nivell d'efectius com a nivell de distribució detallada. L'exemple d'això és que fins l'any 1998 només es censava anualment una de les tres poblacions que presumiblement existien a Espanya (veure revisió a Giralt et al., 2010) i que l'any 1995 es descobria la segona població francesa més important (25 parelles) a prop de Montpeller (Béchet et al., 1995). Així mateix, a Lleida es descobria un petit nucli d'unes 10 parelles l'any 1998 (S. West, com pers; Giralt, 2004), a només 5 km de l'àrea de distribució tradicionalment coneguda, on gairebé ja no hi havia observacions regulars. A Aragó, la única informació disponible era la presència d'alguna parella aïllada, només coneguda per dues o tres persones (A. Bueno, com pers.). Per tot plegat, hi havia una sensació d'incertesa i desconeixement, difícil d'entendre a les portes del segle XXI i en unes zones força poblades d'Europa.

Però l'estat desfavorable de les poblacions occidentals es confirmava a mesura que s'anaven coneixent millor, i el primer avís el va donar la població de Girona, que es va extingir l'any 2002 (capítol 1). En el mateix capítol es quantifica en un 50% la pèrdua de l'àrea de distribució de la població de Lleida en una dècada (entre principis dels anys 90 i principis del segle XX), xifra que arribava al 68% pel conjunt de Catalunya (Giralt, 2004). També a França es reduïa l'àrea de distribució, quan es van perdre petits nuclis al llarg dels anys 90 a la regió de Gard i de La Crau (Lefranc, 1999; Labourye, 2003). Pel que fa a la tendència poblacional, al capítol 1 es quantifiquen per primer cop les tendències poblacionals de la població gironina i francesa: la primera va perdre anualment el 14% dels efectius entre 1993 (9 parelles) i 2002 (cap parella), mentre que la segona va decréixer en un 8% anual entre 1993 (53 parelles) i 2004 (20 parelles), és a dir es confirmava una forta tendència negativa a la zona mediterrània. Finalment, pel que fa a les poblacions de Lleida i d'Aragó (censades anualment a partir del 2002) han seguit un camí similar o pitjor, amb un descens poblacional anual del 29% de mitjana en conjunt (Giralt et al., 2010), des de 2002 (24 parelles) fins al 2010 (1 parella) (capítol 5) (Figura 6). En conjunt, des de l'inici del segle XXI, s'han extingit 2 de les 5 poblacions estudiades en aquesta tesi (capítol 1), una tercera (Lleida) es troba al límit de l'extinció (capítol 5), i les dues franceses continuen en declivi, amb un total de 17 parelles al 2010 (Quaintenne et al., 2014)(Figura 6).

Figura 6: Evolució de les poblacions occidentals de trenca (1989-2010) (Font: Capítol 1; Capítol 5; Lefranc com pers.; Bougarde, com. pers.; Giralt et al., 2010; Quaintenne et al., 2014)



Una de les conseqüències del declivi continuat durant les darreres dècades de les poblacions occidentals de trenca i, més concretament, de la població espanyola, s'ha comprovat a nivell genètic al capítol 4. La variabilitat genètica de la població espanyola és la més baixa en comparació amb les altres poblacions analitzades d'Europa de l'Est (Eslovàquia i Hongria) i d'Àsia (Geòrgia i Kazakhstan). Tant a nivell mitocondrial com a nivell nuclear, s'ha constatat una menor variabilitat a la població espanyola respecte la resta de poblacions europees i asiàtiques estudiades, i la mida efectiva de la població al 2006 era de només 3.9 exemplars. Tot plegat confirma que hi ha hagut una pèrdua genètica com a conseqüència de la fragmentació i aïllament de les poblacions i la reducció dels efectius al llarg de vàries dècades, i a través de la deriva genètica i/o d'un flux genètic molt restringit (baixa o nul·la immigració). La bibliografia recolza aquesta interpretació, ja que parla de dècades de declivi a l'Europa occidental (Lefranc, 1995; Lefranc & Worfolk, 1997). Alternativament, la baixa diversitat genètica podria ser el resultat d'un efecte fundador associat amb una recent colonització de la península, aspecte suggerit per algun autor (Wallace & Sage, 1969), però aquest raonament és molt poc parsimoniós, tenint en compte que hi ha registres antics de trenca del segle XIX a la península (Vayreda, 1883) i que a França està ben documentada la regressió històrica de l'espècie, i cap recolonització substancial (Lefranc, 1995; Lefranc & Worfolk, 1997).

El paper de la intensificació agrícola, la qualitat d'hàbitat i la disponibilitat tròfica en el declivi de les poblacions occidentals

Conèixer quins hàbitats formen part dels territoris de nidificació d'una espècie o població i, sobretot, quins són seleccionats per a obtenir l'aliment, és un aspecte crucial en ecologia, i molt important des del punt de vista de la conservació, per tal d'identificar els requeriments ecològics i, si és necessari, elaborar mesures de gestió de l'hàbitat (Morris, 2003). A més a més, s'ha vist que les espècies més vulnerables i sensibles (major potencial de risc d'extinció) a la degradació i pèrdua d'hàbitat, són aquelles que tenen una mida corporal petita i que mostren un grau d'especialització ecològica major, ja sigui a nivell tròfic com d'hàbitat (Owens & Benett, 2000), característiques que compleix la trenca (Kristín, 1995; Isenmann et al., 2000; Lepley et al., 2004; Hoi et al., 2004). Per això la hipòtesi de partida del capítol 3 era que la disponibilitat d'aliment podia de ser un factor molt rellevant en la selecció de l'hàbitat de cacera i en la composició dels territoris de nidificació. Efectivament, els adults no cacen a l'atzar dins el territori, sinó que seleccionen positivament els hàbitats naturals (matollars, timonedes, etc.) i semi-naturals (guarets i guarets vells) a l'hora d'obtenir l'aliment per ells o pels polls: tot i representar el 23% de la superfície dels territoris, el 71% dels intents de cacera es produïen en aquests hàbitats. La resta d'hàbitats (cultius) eren utilitzats per sota de la seva disponibilitat. A més a més, la selecció de l'hàbitat de cacera ve mediatitzada per la disponibilitat tròfica (capítol 3), ja que la quantitat (biomassa) de coleòpters i ortòpters de mida gran (>20 mm) era entre dos i tres vegades superior en els hàbitats naturals i semi-naturals que als cultius, on els tractaments agrícoles són més freqüents i/o intensos (llaurat, aplicació de fungicides, etc.). De fet, els hàbitats naturals i no cultivats, dins una matriu agrícola intensificada, s'han demostrat importants per molts altres ocells d'aquests ambients, proporcionant aliment, llocs de nidificació i refugi (Benton et al., 2003; Fuller et al., 2004; BirdLife International, 2004).

La selecció de l'hàbitat d'alimentació o cacera en aquesta espècie només havia estat estudiada per Wirtitsch et al. (2001) en una població d'Europa de l'Est (Eslovàquia). Aquests autors trobaven que els adults seleccionaven positivament el sòl nu, és a dir zones sense vegetació (llaurats, clapes dins els cultius, etc.). Això els portava a la conclusió que el factor limitant en aquesta població és l'accés als insectes, més que no pas la seva disponibilitat, donat que l'àrea d'estudi es troba en una zona d'agricultura tradicional i extensiva, amb bones poblacions d'insectes. De fet, tant la disponibilitat com l'accés a les preses són els principals factors (juntament amb el risc de ser depredat) que regulen la selecció d'hàbitat d'alimentació en moltes espècies d'ocells i, en particular, dels que cacen a partir de l'estratègia del "sit & wait" (Beachly et al., 1995).

Que la disponibilitat tròfica és important i un factor limitant en un context d'agricultura intensificada, ho demostra el fet que les parelles produeixen més polls quan tenen hàbitats no cultivats al voltant del niu, al menys les que nidifiquen més aviat (capítol 3). Això concorda amb els resultats del capítol 2, on es constata que aquest és el paràmetre reproductor que difereix entre una població estable d'Europa de l'Est, amb una agricultura més extensiva i major abundància d'insectes, i una població a Europa occidental, en un context més intensificat. En quan a les parelles que nidifiquen més tard, tot i que també seleccionen els hàbitats naturals i semi-naturals per a caçar, no sembla que treguin profit d'aquests hàbitats a nivell reproductiu, potser a causa d'una possible disminució de la disponibilitat d'insectes al llarg de l'estació (propera a la significació). Alternativament, altres factors podrien estar emmascarant i/o limitant el resultat de la reproducció, com per exemple la depredació de nius o limitacions derivades de la curta estació reproductiva de la trenca i del seu comportament migrador de llarga distància (Hemborg et al., 2001).

Per altra banda, hi ha evidències que la pèrdua i degradació de l'hàbitat ha pogut limitar les poblacions occidentals a través d'una manca de llocs òptims per a nidificar, i no només mitjançant la disminució de la qualitat de l'hàbitat d'alimentació. En primer lloc, la densitat de parelles és inferior a les poblacions en declivi (1.4-2.4 parelles/km^2 a Lleida (capítol 1) i 1.7-1.9

parelles/km^2 a França (Bara, 1995), que no pas a la població estable situada a Europa de l'Est (1.8-4.2 parelles/km^2) (Kristín et al., 2000). En segon lloc, les típiques agregacions de parelles descrites per aquesta espècie, també semblen ser de mida més petita a la poblacions occidentals (a Lleida 2.2 parelles/clúster de mitjana (capítol 2)) que les descrites a Europa de l'Est, on per exemple poden ser de fins a 7 parelles (Hoi et al., 1997) o fins i tot de 23 nius en un camp de 17 arbres fruiters (veure revisió a Lefranc, 1993). Una major densitat de nidificació i un major grau d'agregació sovint són indicadors d'una major qualitat de l'hàbitat per moltes espècies (Donahue, 2006; Johnson et al., 2006). De fet, la taxa d'envol de polls (nombre de polls que volen per parella exitosa) és superior per les parelles que s'agreguen que per les parelles que nidifiquen de forma solitària (capítol 2), patró que es repeteix a Europa de l'Est (Kristín et al., 2000), i que podria està reflectint una distribució també agregada d'hàbitats de més bona qualitat (Zanette et al, 2006), tot i que no es pot descartar que l'agregació produeixi beneficis contra la depredació de nius (Isenmann et al., 2000). Finalment, hi ha indicis obtinguts a partir d'aquest treball però no inclosos en la present tesi (Giralt et al., 2010), que indiquen nítidament que l'hàbitat de nidificació és escàs, si més no en els darrers 10 anys i pel cas de la població lleidatana. En aquell treball, es va trobar que la superfície d'hàbitat òptim per a la nidificació a la plana de Lleida només ocupava 8 km^2 d'un total de 2.600 km^2, és a dir menys del 1% de l'àmbit d'estudi (Giralt et al., 2010). No només això, sinó que l'hàbitat es distribuïa de forma molt fragmentada, amb una mitjana de 6.5 ha per taca d'hàbitat òptim, una superfície insuficient (Krsitín, 1995; Wirtitsch et al., 2001) per permetre la formació d'agregacions de parelles, on ja s'ha vist que el resultat de la reproducció, és superior. En definitiva, diverses evidències suggereixen que la pèrdua d'hàbitat de qualitat pot haver limitat l'establiment de parelles i la formació d'agregacions i, per tant, que pot haver contribuït al declivi de la població.

En resum, si com indica una extensa bibliografia (De Juana et al., 1988; Krebbs et al., 1999; Chamberlain et al., 2000; BirdLife International, 2004), la intensificació agrícola ha comportat la davallada de els poblacions d'insectes i un canvi d'usos (pèrdua de mosaics agrícoles amb vegetació natural, més terra en producció i menys guarets, expansió de monocultius, etc.), els resultats dels capítols 2 i 3 donen total suport a la idea que el declivi de la trenca a Europa occidental ha estat propiciat, al menys en part, per aquest procés, tal i com ha passat amb altres espècies de medis agrícoles (Campbell et al., 1997; BirdLife International, 2004; Hart et al., 2006). Resultats similars per altes lànids s'han obtingut arreu d'Europa, demostrant l'efecte perjudicial de la intensificació agrícola sobre característiques clau de l'hàbitat i sobre l'estat de conservació d'aquest grup d'ocells (BirdLife International, 2004; Brambilla et al., 2007; Kuczynski et al., 2010).

Sincronia espacial, canvi climàtic i variabilitat ambiental com a possibles causes de regressió a la perifèria de l'àrea de distribució

La detecció d'una sincronia espacial en les fluctuacions interanuals de la mida de les poblacions de Girona i França, situades a menys de 300 km les unes de les altres, suggereix que un factor comú les regula (capítol 1), fet que suposa una major vulnerabilitat davant un procés d'extinció. La meteorologia és un factor sincronitzador reconegut (Paradis et al., 2000; Williams et al., 2003; Liebhold et al., 2004) i factors denso-independents, com els meteorològics, poden tenir una gran influència en els paràmetres demogràfics de poblacions perifèriques (Hoffmann & Blows, 1994; Williams et al., 2003). Per tant, és possible que la posició perifèrica pugui haver contribuït a la dinàmica de les poblacions occidentals, però aquest aspecte caldria resoldre'l analitzant altres poblacions, ja que en el cas de les estudiades en aquesta tesi, l'efecte de la perifèria es pot confondre amb altres problemàtiques, com ara una mida poblacional petita.

En relació a si factors meteorològics i ambientals poden provocar aquesta sincronia espacial, a partir d'un anàlisi correlatiu, s'observa que les fluctuacions interanuals (1989-2002) de la mida de la població de Girona anaven íntimament lligades a l'oscil·lació tèrmica i a l'índex de desenvolupament vegetal (NDVI) en aquella àrea: a més oscil·lació tèrmica o menys vegetació (o més seca) a la primavera, menys parelles nidificants (capítol 1). A més a més, la població de Girona també mostrava una relació (negativa) amb l´índex de desenvolupament vegetal a l'àrea d'hivernada (sud d'Àfrica): a més vegetació (o menys seca), menys parelles nidificants. El patró correlatiu observat a Girona entre les variables ambientals i les fluctuacions interanuals de la població, és més dèbil a França, ja que només una de les poblacions franceses es veu afectada per l'índex de desenvolupament vegetal, però en aquest cas pel d'una població veïna, la gironina (capítol 1). Potser a França no s'han trobat relacions més fortes degut a interaccions entre el clima i factors locals (Ringsby et al., 2002) o degut a una sèrie de dades massa curta.

El paper de l'índex de desenvolupament vegetal sobre la trenca i altres espècies (Sanz et al., 2003) mereix atenció, ja que Giralt et al. (2010) també comproven que el valor del mateix índex a l'inici de l'etapa reproductiva (maig), és una de les variables més rellevants a l'hora de definir la qualitat de l'hàbitat de la població de Lleida: a valors més alts de vegetació (però no màxims), major qualitat de l'hàbitat. El mecanisme pel qual aquests paràmetres meteorològics i ambientals podrien estar limitant l'establiment de parelles nidificants a Girona podria ser directe (afectant aspectes fisiològics relacionats amb la reproducció, resposta immune, etc.) (Pörtner & Farrell, 2008) o indirecte, a través de la disponibilitat d'insectes, per exemple degut a un avançament fenològic del pic de producció (Peñuelas et al., 2002; Sanz et al., 2003; Both et al., 2006), al qual una espècie de llarga migració difícilment es pot adaptar (Herremans, 1998b; Both et al., 2006; Rubolini et al., 2010).

Per altra banda, es detecten tendències significatives a nivell climàtic pel període 1989-2002, per les mateixes variables que es correlacionen amb l'abundància: un increment de l'oscil·lació tèrmica i una disminució de l'índex de desenvolupament vegetal (NDVI) durant l'època de nidificació (maig-juny) a l'àrea de Girona. Aquestes dades indiquen que aquella zona cada any és més seca i tèrmicament contrastada, durant la primavera. Aquests resultats venen corroborats a nivell de tot Catalunya (http://static-m.meteo.cat/wordpressweb/wp-content /uploads/ 2015/06/ 05083250/BAIC2014_Resum_ executiu.pdf), especialment pel que fa a les temperatures mitjanes i màximes, des de 1950 fins a l'actualitat. Més concretament també es detecta aquest canvi a la costa de Girona (Piñol et al., 1998; http://www.meteo.cat /wpweb/climatologia/el-clima-ara/tendencia-climatica/ tendencia-series/). De fet, també està comprovat l'increment de temperatures a la primavera i a l'estiu al sud-est de França (on es situen les poblacions de trenca), durant les darrers dècades (Chuine et al., 1998; Spagnoli et al., 2002; Fréjaville & Curt, 2015).

El paper de la meteorologia i del canvi climàtic com a possible causa del declivi de les poblacions occidentals, requereix de més estudis per confirmar-se, però el seu paper regulador és probable, vista la sincronia espacial entre les poblacions de Girona i França en el període 1993-2002 i les correlacions trobades amb variables meteorològiques a Girona i en una població francesa. Alternativament, és difícil pensar que alteracions de l'hàbitat (d'origen antròpic) a les tres àrees de nidificació (Girona, Aude i Montepller) siguin les responsables d'aquesta sincronia. Liebhold et al., (2004) revisen el fenomen de la sincronia en la dinàmica de poblacions i mencionen tres causes o mecanismes principals, molts cops difícils d'estudiar i d'identificar: 1) la dispersió d'exemplars entre poblacions governades pel mateix procés denso-dependent, 2) factors exògens, amb la meteorologia i el clima com a principals agents i 3) interaccions tròfiques amb poblacions d'altres espècies que es veuen regulades o bé per la dispersió o bé per factors exògens. Per tant, per anar més enllà, caldrien estudis que comparessin un major nombre de poblacions i que analitzessin simultàniament el paper de la meteorologia i la dispersió.

Mecanismes demogràfics del declivi i risc d'extinció

Més enllà de les causes que han pogut causar la fragmentació i disminució de les poblacions de trenca i l'extinció d'algunes d'elles, és important entendre els mecanismes demogràfics que, en última instància, han portat a aquesta situació. Als capítols 2 i 3 hem fet èmfasi en els paràmetres reproductius com un possible mecanisme del declivi: la taxa d'envol és l'únic paràmetre que difereix entre la única població en bon estat de conservació d'on es disposa d'aquesta informació (situada a prop de l'àrea central de la distribució) (Kristín et al., 2000) i les poblacions perifèriques de Lleida (capítol 2) i de Montpeller (França) (Isenmann & Debout, 2000). Més en detall, la taxa d'envol és inferior degut a les pèrdues d'ous (ous desapareguts o no eclosionats) i, sobretot, degut a al mortalitat dels polls durant els 15-16 dies que estan al niu, ja que el 61% dels nius perden al menys 1 poll i el 19% dels polls que neixen, moren o desapareixen durant aquest breu període de temps (capítol 2). Per tant, des d'un punt de vista comparatiu, aquest és l'únic paràmetre reproductor que podia haver contribuït al diferent estat de conservació entre les poblacions perifèriques i la central. Malgrat això, el seu impacte sobre la taxa de creixement i la probabilitat d'extinció de les poblacions és baix i per tant, aquest no pot ser l'únic mecanisme ni el més important (capítol 5, veure més endavant).

Per altra banda, el percentatge d'èxit reproductor, és a dir la proporció de parelles que treuen endavant un poll (com a mínim) respecte el total de parelles que realitzen posta (parelles nidificants), no va variar massa entre la població central d'Eslovàquia (26% de mitja) (Kristín et al., 2000) i la catalana (33% de mitja) (capítol 2). A la població francesa de Montpeller també es van registrar dades similars, fins i tot inferiors (15%) (Isenmann et al., 2000). Els valors d'aquestes taxes tant similars entre elles, i el fet que la principal causa de fracàs també sigui la mateixa (depredació), fa difícil pensar que aquest paràmetre sigui un possible mecanisme per explicar l'estat de conservació diferent entre aquestes poblacions. A més a més, són valors acceptables i habituals per una espècie d'ocell que nidifica en nius oberts i lluny del terra (Martin & Li, 1992). Independentment que els valor absoluts i les dades comparatives, així com la modelització demogràfica (capítol 5; veure més endavant), suggereixin que l'èxit reproductor té poca rellevància en el declivi de les poblacions occidentals de trenca actuals, val a dir que la depredació de nius pot representar un factor regulador important quan les poblacions són molt petites o es troben molt fragmentades (Chalfoun et al., 2002). En aquest sentit, la probabilitat de fracàs d'un niu de trenca depèn de la proximitat de nius de garsa (*Pica pica*) a l'àrea de nidificació de Lleida, on aquesta espècie és molt abundant (capítol 2). En canvi, a una escala espacial més gran, no detectem cap correlació entre la taxa de predació i la densitat de garsa. Altres autors han detectat relacions espacials entre els territoris del depredador i els nius de les seves preses (Andrén, 1990; Roos & Pärt, 2004).

En força espècies o poblacions d'ocells s'ha pogut comprovar com el mal resultat de la reproducció era el responsable d'una tendència poblacional negativa (Donovan et al., 1995; Potts & Aebischer, 1995; Peery et al., 2004), però també la supervivència juga un paper determinant per la viabilitat de moltes espècies amenaçades, sobretot per aquelles de llarga longevitat (Owens & Bennett, 2000; Purvis et al., 2000). Altres mecanismes demogràfics, com els nivells d'immigració que rep una població, també poden ser determinants en la dinàmica d'una població (Morris & Doak, 2002; Schaub et al., 2013). Per tant, al capítol 5 vam voler explorar la contribució relativa que tenien sobre la dinàmica poblacional, els paràmetres reproductius en comparació amb les taxes de retorn anual d'adults i joves, assumint que la immigració d'exemplars des d'altres poblacions era nul·la (capítol 4). D'aquesta manera, mitjançant un anàlisi de viabilitat poblacional que integrava el màxim d'informació demogràfica, també podríem entendre quina seria la possible efectivitat d'implementar diferents mesures de gestió dirigides a millorar determinats paràmetres demogràfics, mesurant l'impacte d'aquestes millores sobre la taxa de creixement o la probabilitat d'extinció. Els paràmetres analitzats van ser la taxa d'envol, l'èxit reproductor i la taxa de retorn d'adults i individus de primer any (percentatge d'ocells que tornen a la població l'any *t*, respecte els que han marxat l'any *t-1)*. Així doncs, si cap paràmetre no canviava de forma substancial respecte el període d'estudi (2002-2005), el model bàsic preveia una altíssima probabilitat d'extinció (98%) de la població lleidatana en deu anys (2006-2016). Els resultats del capítol 5 també indicaven que els paràmetres reproductors (taxa d'envol i èxit reproductor) tenien una influència mínima sobre la taxa de creixement i la probabilitat d'extinció: per exemple, si la taxa d'envol passava a ser de 5 polls/parella i l'èxit reproductor del 90% (per exemple a través d'una gestió molt intensiva mitjançant alimentació suplementària i control de depredadors de nius), la probabilitat d'extinció continuava sent molt elevada, del 79% a 10 anys vista (i la taxa de creixement negativa). En canvi, una millora del 30% de la taxa de retorn dels adults o dels joves, ja reduïa la probabilitat d'extinció de la població al 12% i al 17%, respectivament, al cap de 10 anys. Així doncs, la principal conclusió era que assumint que no hi havia immigració a la població de Lleida, les taxes de retorn observades eren massa baixes per mantenir viable la població i havien de ser les principals responsables del declivi, mentre que les taxes reproductives, tenien menys importància en la dinàmica d'aquesta població. Aquesta predicció es va corroborar, en part, a partir de les dades de camp recollides en anys posteriors (2006-2008), ja que l'èxit reproductor va passar del 69% al 90% de mitjana després de 2005 (probablement degut a un control molt intensiu sobre la població de garsa (*Pica pica*)), sense cap efecte sobre la dinàmica de la població. De fet la població de Lleida només tenia 1 parella nidificant, l'any 2010.

La taxa de retorn inclou la supervivència real més la filopàtria, ja que a partir d'ocells marcats amb anelles, no es pot saber quins han mort i quins han decidit canviar de població. Per tant, el mecanisme demogràfic exacte que ha tingut major impacte sobre la taxa de creixement i la probabilitat d'extinció no el podem conèixer, però sí que es pot descartar que els paràmetres reproductius siguin els principals responsables directes del declivi des de principis del segle XXI, al menys per la població de Lleida. Curnutt et al., (1996) ja mostren que els patrons de dispersió (emigració i immigració) juguen un paper molt rellevant en poblacions perifèriques, més que no pas la reproducció i la supervivència en sí mateixes. Així mateix, no podem descartar que hagin actuat processos denso-dependents, per exemple a través de l'efecte Allee, fent que la filopàtria (i, per tant, les taxes de retorn observades) s'hagin anat reduint a mesura que la població s'anava fent petita (Courchamp et al., 1999), i més tenint en compte el caràcter semi-colonial d'aquesta espècie (Lefranc, 1993) i la utilització d'informació conspecífica comprovada recentment (Hoi et al., 2012).

Cal remarcar que hem assumit una immigració nul.la, donats els resultats genètics trobats al capítol 4 i l'aïllament geogràfic des de fa dècades (capítol 1; Lefranc & Worfolk, 1997) de la població de Lleida i de la resta de poblacions occidentals. Recentment, s'ha comprovat la importància vital de la immigració per a la supervivència i el manteniment d'una població europea d'Escorxador (*Lanius collurio*) (Schaub et al., 2013), una espècie ecològica i taxonòmicament molt similar a la trenca. Per la seva banda, Kristín et al., (2007b) també arriben a la conclusió que el paper de la dispersió (emigració i immigració) ha de jugar un paper rellevant a la població eslovaca, on observen un recanvi interanual substancial dels individus i dels seus territoris de nidificació, i on la taxa de retorn es va estimar en xifres molt similars a les trobades a la població perifèrica de Lleida (40% pels mascles i 25% per les femelles adultes). Tot plegat suggereix que el paper rellevant de les taxes de retorn a la població de Lleida, podria ser un reflex de l'aïllament geogràfic i la fragmentació de les poblacions, i que un balanç desfavorable entre immigració i emigració, juntament amb processos denso-dependents (efecte Allee), podrien haver contribuït de forma substancial al declivi d'aquestes poblacions, al menys en els darrers anys o dècades. Caldrien més estudis, però, per quantificar el paper dels processos dispersius i densodependents en la fragmentació i declivi d'aquestes poblacions perifèriques.

Finalment, cal parlar de l'estocasticitat com a mecanisme regulador de la dinàmica de poblacions i com a factor de risc d'extinció, especialment en poblacions petites (Caughley, 1994). Pel que fa a l'estocasticitat ambiental, el seu paper pot haver estat rellevant si es confirmés la relació causa-efecte entre el clima i la forta sincronia espacial entre les poblacions de Girona i França (capítol 1). En el cas concret de la població de Girona, les correlacions trobades amb variables meteorològiques i amb l'índex de verdor vegetal suggereixen una gran vulnerabilitat davant l'estocasticitat ambiental i, de fet, la meteorologia també era la principal causa de fracàs reproductor en aquella població (capítol 2). A més a més, la sincronització espacial en sí mateixa, incrementa el risc d'extinció, ja que en anys dolents, les abundàncies baixen a totes les poblacions, posant en perill el global de la població (Palmqvist & Lumberg, 1998; Liebhold et al., 2003). En relació a l'estocasticitat genètica, al capítol 4 es comprova el seu impacte sobre la població espanyola (pèrdua de diversitat genètica) a través de la deriva genètica i/o la manca d'intercanvi d'exemplars amb altres poblacions, molt probablement a causa del llarg declivi i fragmentació soferts per les poblacions perifèriques de trenca. En darrer lloc hi ha l'estocasticitat demogràfica, difícil d'identificar però probable en poblacions molt petites (Caughley, 199; Hanski, 1999): a partir de les dades d'aquesta tesi no es pot confirmar el seu impacte sobre la població, però el sobtat biaix en el sex-ratio (a favor de les femelles) a la població de Lleida a partir de l'any 2008 (només 4 parelles i diverses femelles desaparellades), coincidint amb una baixíssima taxa de retorn, podria ser un símptoma que, per qüestions d'atzar, aquell any van morir o emigrar la majoria de mascles de la població (capítol 5).

Implicacions per a la conservació

De la present tesi es desprèn que la millora de l'hàbitat a diferents escales espacials hauria de ser la prioritat des del punt de vista de la gestió i conservació de les poblacions occidentals de trenca (capítols 2, 3 i 4). A una escala local, aquesta millora hauria d'anar encaminada a conservar i promocionar hàbitats que puguin mantenir poblacions importants d'insectes (sobretot ortòpters i coleòpters) de mida mitjana i gran (>20 mm), assegurant una disponibilitat d'aliment suficient per minimitzar la mortalitat de polls i maximitzar la taxa d'envol. En el cas de la població de Lleida, aquests hàbitats són els guarets i els retalls de vegetació natural (matollars amb poca cobertura vegetal) i haurien d'ocupar al menys el 20% de la superfície dels territoris de nidificació (uns 150 m de radi al voltant del niu). Altres estudis també mencionen la importància d'aquests hàbitats naturals i semi-naturals en la matriu agrícola, especialment en el context d'una agricultura intensiva com la d'Europa occidental (Isenmann & Debout, 2000; Benton et al., 2003; Fuller et al., 2004; BirdLife International, 2004). En un context d'una agricultura més extensiva, els propis usos agrícoles (cultius, prats, etc.) podrien proporcionar suficient aliment (Kristín, 1995; Wirtitsch et al., 2001).

Però seria suficient una gestió de l'hàbitat aplicada només als territoris de nidificació coneguts dels darrers anys, per millorar només la taxa d'envol? Molt probablement no. En primer lloc, l'hàbitat òptim actual, al menys a la plana de Lleida, és molt escàs i fragmentat, és a dir que la capacitat de càrrega actual podria limitar un potencial creixement de la població (Giralt et al. 2010). Per tant, caldria un esforç de recuperació de l'hàbitat més enllà dels territoris de nidificació dels últims deu anys, establint corredors i zones òptimes de suficient superfície com perquè es pugui facilitar l'atracció de conspecífics (Hoi et al., 2012) i formar les típiques agregacions de parelles (Lefranc, 1993), sobretot si pot ser beneficiós pel resultat de la reproducció (capítol 2; Isenmann et al., 2000). Aquesta millora d'hàbitat hauria d'incloure usos rics en insectes (capítol 3), però també arbres per a la nidificació en les proximitats, binomi que actualment és escàs (Giralt et al., 2010). Finalment, però segurament molt rellevant, donat que la immigració sembla ser un paràmetre important pel manteniment de poblacions perifèriques i de la seva diversitat genètica (capítol 4; Curnutt et al., 1996; Schaub et al., 2013), idealment, caldria anar més enllà i fer un esforç de coordinació entre diferents regions i països per tal de crear corredors d'hàbitat adequat de més abast geogràfic i reduir l'actual fragmentació de les poblacions, per tal de facilitar aquest intercanvi d'exemplars. Segons els resultats d'aquesta tesi, aquesta gestió a gran escala seria la única manera de fer autosuficients les poblacions i evitar-ne l'extinció i, molt probablement, fa molt anys (segurament dècades) que s'hauria d'haver iniciat, ja que actualment representaria un esforç de conservació immens que caldria valorar seriosament (Botrill et al., 2008).

Què s'ha fet fins ara, per a la conservació de la trenca? En el marc del paradigma de la població petita (Caughley, 1994), la necessitat més imperiosa és augmentar la mida de la població de forma urgent, a vegades sense saber amb detall la identitat ni la importància relativa de les causes que han portat una població o espècie a aquella situació crítica. En aquest sentit, a la població de Lleida es van implementar mesures de gestió in-situ, des de l'any 2006, com l'alimentació suplementària de les parelles nidificants i el control de qui, aparentment, era el principal depredador de nius, la garsa (*Pica pica*) (capítol 2; capítol 5, Kristín et al., 2000). La primera mesura anava encaminada a la millora de la taxa d’envol i la segona a la millora de l’èxit reproductor. L’efectivitat d’aquestes mesures no s’ha abordat directament en la present tesi per falta de suficient dades, però sembla que la primera mesura no va acabar de funcionar, mentre que la segona sí (capítol 5; dades pròpies no publicades). Una altra mesura d’urgència que sovint s’aplica en aquestes situacions és la gestió ex-situ, per exemple a través de la cria en captivitat i el posterior alliberament d’exemplars per reforçar (o reintroduir) la població salvatge. La trenca no és una excepció i l’any 2007, els serveis territorials de Medi Ambient de Lleida van iniciar aquest projecte, fet que segurament permet entendre perquè la població de Lleida encara no s’ha extingit avui en dia (2 parelles nidificants l’any 2015). Existeix molta controvèrsia al voltant dels projectes de cria en captivitat (Bowkett, 2009). En primer lloc perquè, com en el cas que ens ocupa, sovint es duen a terme sense haver aplicat mesures de gestió in-situ (gestió de l’hàbitat, etc.) com es recomana des de la UICN (IUCN/SSC, 2014). En segon lloc perquè, com en el cas de l’alimentació suplementària, es poden convertir en trampes de conservació (Cardador et al., 2015): com que no resolen les causes últimes del declivi, quan es deixen d’aplicar la població torna a entrar en situació crítica. Per tant, tot i ser mesures comprensibles i necessàries quan la població és molt petita, no s’haurien de perpetuar excessivament en el temps i haurien d’aplicar-se en paral·lel a les mesures que resolen directament les causes del declivi. Caldrà veure com evoluciona en el futur la població de Lleida, però si les baixes taxes de retorn i, possiblement, la manca d’immigració han jugat un paper important en el seu declivi (capítol 5), no sembla que cap d’aquestes mesures d’urgència, per elles soles, puguin ser efectives a mig i llarg termini.

En la present tesi s’ha intentat considerar el paradigma de la població en declivi, estudiant les causes i els mecanismes del declivi mitjançant estudis comparatius entre poblacions en bon i en mal estat de conservació (capítol 2), o intentant relacionar determinats factors biòtics (disponibilitat de preses) o abiòtics (variabilitat ambiental) amb paràmetres demogràfics o poblacionals (capítols 1 i 3)(Caughley, 1994; Peery et al., 2004), per tal de dirigir de manera més eficient la gestió i conservació (capítol 5) (Morris & Doak, 2002). Tant el paradigma de la població petita com el de la població en declivi són sovint necessaris en la conservació de poblacions o espècies molt amenaçades, però la conclusió evident és que en la disciplina de la biologia de la conservació, és recomanable ser previsor (mitjançant programes de seguiment i de conservació) i no arribar a situacions poblacionals crítiques, ja que aleshores és molt més difícil identificar i revertir els efectes de diferents factors deterministes i estocàstics que estan actuant de manera simultània sobre la dinàmica poblacional (Simberlof 1986; Caughley, 1994).

La present tesi és un exemple de situació crítica en biologia de la conservació, i malgrat que s'ha avançat en la comprensió de les causes i mecanismes del declivi poblacional, la baixa mida mostral amb la que s'ha treballat des de l'inici ha dificultat una millor comprensió de tots els factors implicats i, en alguns casos no ha permès aprofundir en alguns aspectes, com per exemple en el paper relatiu de la mortalitat i de la dispersió en les taxes de retorn observades. No només això, sinó que en el temps necessari per recollir la informació requerida i per entendre la dinàmica poblacional i prendre decisions, la majoria de poblacions s'han extingit o estan a punt de fer-ho.

Finalment, un cop repassades les implicacions per a la conservació que es desprenen de la tesi, ens podem preguntar si cal conservar les poblacions occidentals de trenca, tenint en compte que la situació actual és realment crítica (21 parelles el 2015, entre França i Espanya), i considerant que, aparentment, aquesta espècie encara manté bones poblacions a Europa de l'Est i, especialment a Àsia. Des d'un punt de vista de les diferenciació genètica (capítol 4), la població espanyola podria tractar-se com una "unitat de gestió" (MU) d'acord amb Moritz (1994), però no com una "unitat evolutiva significativa" (ESU) (Moritz, 1994). És a dir que, des d'un punt de vista evolutiu, sembla que la població espanyola no tindria un potencial adaptatiu diferent al d'altres poblacions europees (Moritz, 1994; Crandall et al., 2000). Tampoc hi ha massa suport per la diferenciació de les dues subespècies de trenca proposades per algun autor (una europea i una asiàtica) i caldria analitzar més poblacions per descartar que l'estructura genètica trobada (una europea i dues asiàtiques), no sigui en realitat una clina. Hi ha altres criteris també vàlids, apart dels genètics, per decidir si val la pena conservar una espècie o població: de tipus ètic, cultural, econòmic, legal, etc. (Shrader-Frechette & McCoy, 1994; Botrill et al., 2008). De totes maneres, tenint en compte que els recursos disponibles per a la conservació són limitats y que ritme actual d'extinció d'espècies i de pèrdua de biodiversitat és descomunal, recentment va guanyant terreny el concepte més pragmàtic del "triage", que significa prioritzar els esforços de conservació segons els beneficis obtinguts, els costos que impliquen i la probabilitat d'èxit de les diferents alternatives de conservació (Botrill et al., 2008). Seguint aquests darrers criteris i amb la informació aportada en aquesta tesi i en altres estudis, continuar dedicant esforços a la recuperació de la trenca a Europa occidental no sembla la millor opció. Al final, però, la conservació acaba sent sempre una qüestió subjectiva. Espero que, amb tots aquest ingredients a sobre la taula i després de llegir la present tesi, el lector tindrà, al menys, més informació per formar-se una opinió sobre si cal o no conservar les poblacions occidentals de trenca actuals i les d'altres espècies que puguin estar en situacions i problemàtiques similars.

CONCLUSIONS

1. Totes les poblacions franceses i espanyoles han reduït la seva àrea de distribució des de 1990, al menys en un 50% de la seva superfície. Entre 1993 i 2002, la tendència de les dues poblacions franceses i la de la gironina ha estat clarament negativa i la darrera es va extingir el 2002. En el període 2001-2010 també la població de Lleida ha mostrat una tendència negativa, i al 2010 ja només mantenia 1 parella nidificant.

2. La població espanyola és la que mostra menys diversitat genètica de totes les poblacions europees i asiàtiques analitzades. La pèrdua genètica s'hauria produït a través de la deriva genètica i/o d'una disminució en l'intercanvi d'exemplars entre poblacions. L'existència d'observacions històriques de l'espècie a Catalunya i el declivi documentat, descartaria que la baixa diversitat genètica sigui conseqüència d'un efecte fundador produït per una recent colonització (anys seixanta).

3. L'anàlisi genètic identifica tres grans grups o unitats evolutives (ESU) dins l'àrea de distribució: un d'europeu i dos d'asiàtics, fet que aconsella una reavaluació de les dues subespècies (una europea i una asiàtica) considerades per alguns autors. Aquesta diferenciació en tres grups coincideix amb el patró de migració pre-nupcial entre Àfrica i Euràsia, que obliga als individus a separar-se en tres direccions diferents un cop arriben a la península aràbiga.

4. Hi ha evidències de tipus correlacional que variables climàtiques (increment de l'oscil·lació tèrmica) i la reducció de l'índex de desenvolupament vegetal (NDVI) a l'àrea de nidificació perifèrica, han contribuït a la sincronia espacial observada. A més a més s'observa una progressiva pèrdua del desenvolupament vegetal al llarg dels anys a una de les àrees de nidificació i altres estudis comproven un increment tèrmic a les zones ocupades per les tres poblacions.

5. Les dues poblacions franceses i la gironina mostren una forta sincronia espacial en les fluctuacions interanuals de la mida de la població (nº de parelles reproductores) entre 1993 i 2002. Aquest fet indica l'existència d'un factor comú que les regula que, en consonància amb la conclusió anterior, pot estar relacionat amb l'increment tèrmic descrit en les zones ocupades per les tres poblacions y/o amb una progressiva pèrdua del desenvolupament vegetal en zones clau per l'espècie.

6. Es confirma la importància de la disponibilitat tròfica en el comportament de cacera i en el resultat reproductiu de les parelles. Els adults seleccionen per a caçar els hàbitats que ofereixen major disponibilitat d'insectes de mida gran: hàbitats naturals (matollars) i semi-naturals (guarets). Els usos del sòl pròpiament agrícoles com el cereal i els fruiters, tenen menys disponibilitat d'aliment i són utilitzats menys de l'esperat o, directament, evitats.

7. La taxa d'envol (nº polls/parella exitosa) de les parelles més primerenques es veu positivament influenciada per la superfície d'hàbitats amb major disponibilitat d'insectes de mida gran al voltant del niu (vegetació natural i semi-natural). Per contra, les parelles més tardanes, tot i que també seleccionen positivament aquests hàbitats per anar a caçar, no es veuen beneficiades en termes reproductius.

8. La trenca pot nidificar de forma semi-colonial, formant agregacions, on la taxa d'envol de polls és superior respecte la de les parelles que nidifiquen de forma aïllada. A més a més, les agregacions de parelles són més petites a la població perifèrica que a la central. És important aclarir els factors que regulen la mida de les agregacions, ja que poden estar indicant les zones més òptimes o adequades per l'espècie.

9. L'únic paràmetre reproductiu que difereix entre una població perifèrica (Catalunya) i una població cèntrica (Eslovàquia) de trenca és la taxa d'envol de polls (inferior a la perifèrica). No obstant, l'anàlisi de viabilitat poblacional mostra que la taxa d'envol té molt poca influència sobre la taxa de creixement i sobre la viabilitat poblacional i, per tant, no pot ser l'únic mecanisme del declivi de les poblacions perifèriques ni el més important.

10. La depredació de nius és la principal causa de fracàs, tant a la perifèria com a l'àrea de distribució cèntrica. La probabilitat de fracàs d'una parella augmenta a mesura que disminueix la distància als nius d'un depredador molt abundant en aquestes zones, la garsa (*Pica pica*). No obstant, l'anàlisi de viabilitat poblacional indica que aquest paràmetre tampoc és el més rellevant en relació a la viabilitat de les poblacions de trenca.

11. Assumint una nul.la immigració, la taxa de retorn (supervivència i filopàtria), tant d'adults com de joves, és el paràmetre més rellevant per a la supervivència de les

poblacions i evitar-ne l'extinció. Per tant, una estratègia de conservació basada només en la millora dels paràmetres reproductius a nivell local no tindria efectes rellevants sobre el futur d'aquestes poblacions.

12. Si és considerés oportú continuar dedicant esforços de conservació per a les poblacions occidentals de trenca, la principal mesura de gestió a aplicar hauria de ser la millora de l'hàbitat a diferents escales espacials: 1) a escala de territori de nidificació, per tal de potenciar els hàbitats de més qualitat, la disponibilitat d'insectes i la taxa d'envol i 2) a escala de totes les poblacions (establint corredors) per tal d'afavorir l'intercanvi d'exemplars i la immigració des de poblacions més grans.

13. De cara a futurs estudis, és prioritari aclarir el paper de la immigració, la supervivència, la filopàtria i l'existència de possibles efectes denso-dependents sobre la taxa de retorn. És igualment important estudiar la situació de l'espècie a l'àrea d'hivernada i durant la migració, etapes que ocupen bona part de la vida dels individus. Tota aquesta informació també seria rellevant per a la conservació de poblacions que encara es troben en bon estat de conservació o que tot just comencen a estar en declivi.

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CAPÍTOLS

CAPÍTOL 1

Population trends and spatial synchrony in peripheral populations of the endangered Lesser grey shrike in response to environmental change

Tendències poblacionals i sincronia espacial en poblacions perifèriques i amenaçades de la trenca, en resposta a canvis ambientals

Giralt, D. & Valera, F., 2007. Population trends and spatial synchrony in peripheral populations of the endangered Lesser Grey Shrike in response to environmental change. Biodiversity and Conservation 16: 841-856.

Tendències poblacionals i sincronia espacial en poblacions perifèriques i amenaçades de la trenca, en resposta a canvis ambientals

David Giralt Jonama i Francisco Valera Hernández

RESUM: La sincronització regional de la dinàmica de les espècies, així com les característiques ecològiques i demogràfiques particulars de les poblacions perifèriques, planteja especials desafiaments per a la conservació, especialment en el marc de l'actual escenari de canvi climàtic i canvi global. En aquest treball s'estudia la tendència poblacional i la sincronia espacial de diverses poblacions perifèriques situades al límit occidental de l'àrea de reproducció (sud de França i nord-est d'Espanya) de trenca (*Lanius minor*), espècie amenaçada. Per tal d'intentar determinar l'efecte dels canvis ambientals en el declivi de l'espècie també busquem evidències del canvi climàtic en la seva àrea de nidificació i d'hivernada, així com els seus efectes sobre la vegetació, mitjançant l'índex de verdor de la vegetació (NDVI). Hem trobat que les fluctuacions interanuals de la poblacions perifèriques a França i Espanya estan fortament correlacionades, fet que suggereix que la seva disminució pot estar sota la influència d'un factor comú. Hem obtingut una clara evidència de canvi climàtic (un augment de l'oscil·lació tèrmica) en una de les poblacions perifèriques que pot haver donat lloc a la disminució de l'índex NDVI a la zona. En el nostre estudi trobem evidències correlacionals que les variables climàtiques en l'àrea de nidificació poden explicar les fluctuacions en l'abundància d'algunes poblacions i que les condicions ambientals experimentades per alguna població podrien influir el destí de les poblacions veïnes. Els nostres resultats indiquen que les poblacions perifèriques estudiades estan espacialment sincronitzades, fet que implica que els esforços de conservació haurien de ser aplicats a gran escala, incloent totes aquestes poblacions aïllades situades al límit occidental de l'àrea de distribució de la regió mediterrània.

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ORIGINAL PAPER

Population trends and spatial synchrony in peripheral populations of the endangered Lesser grey shrike in response to environmental change

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Abstract Regional synchronization in species dynamics as well as particular ecological and demographic characteristics of peripheral populations poses special challenges for conservation purposes, particularly under the current scenario of global climate change. Here, we study the population trend and spatial synchrony of several peripheral populations of the endangered Lesser grey shrike *Lanius minor* at the western limit of its breeding range (southern France and northeast Spain). In an attempt to ascertain the effect of environmental change on the decline of the species we also look for evidence of climate changes in the breeding and wintering area of this shrike and related effects on vegetation by using the normalized difference vegetation index (NDVI). We found that the interannual fluctuations of the peripheral populations in France and Spain are strongly correlated, therefore suggesting that their decline can be under the influence of a common factor. We obtained clear evidence of climatic change (an increased thermal oscillation) in one peripheral population that could have resulted in a decrease of the NDVI index in the area. Our study finds correlational evidence that climatic variables in the breeding area may account for fluctuations in abundances of some populations and that environmental conditions experimented by some population could influence the fate of the neighboring populations. Our results indicate that the studied peripheral populations are spatially synchronized, so that conservation efforts should be applied at a large-scale encompassing all the isolated populations at the western border of the range of the species in the Mediterranean area.

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Keywords *Lanius minor* · Mediterranean region · Population trend · Range periphery · Spatial synchrony

Introduction

Understanding the spatial distribution of organisms is a crucial issue in population dynamics (Tilman and Kareiva 1997) and has important consequences for more applied sciences such as conservation biology, where strategies for long-term species conservation depend on present and future patterns of abundance (Lawton et al. 1994; Brown et al. 1995; Mehlman 1997; Williams et al. 2003). One major topic in this field is the comprehension of the abundance distribution within the range of a given species and the roles of density-dependent and density-independent processes in determining the variability of population abundances (Hengeveld and Haeck 1982; Brown 1984; Royama 1992; Mehlman 1997; Williams et al. 2003). It is well-known that peripheral populations, frequently relatively small and isolated from central populations (Lawton 1993; Lesica and Allendorf 1995), are likely to experience different regimes of natural selection than central ones, since the relative importance of abiotic and biotic factors on distribution patterns and population limitation are likely to change according to the position within the geographical range (Randall 1982; Hoffmann and Blows 1994; Brown et al. 1995; Williams et al. 2003). There is evidence supporting the fact that environmental changes and abiotic, density-independent factors, like weather, have a higher influence on demographic rates and produce greater fluctuations in peripheral populations than in central ones (Hoffmann and Blows 1994; Brown et al. 1995; Curnutt et al. 1996; Williams et al. 2003), probably because closeness to the edge of range usually indicates poorer environmental conditions for a species (Brown 1984; Brown et al. 1995). Thus, in the present scenario of climate change (Parmesan et al. 1999; Hughes 2000), we would expect peripheral populations of organisms to be under a stronger influence of environmental changes than populations closer to the core of their range.

An additional factor of uttermost importance in the conservation of peripheral populations and/or of rare or endangered species is spatial synchrony in the dynamics of local populations (Kendall et al. 2000). Spatial synchrony refers to coincident changes in the abundance or other time-varying characteristics of geographically disjunct populations (Liebhold et al. 2004). Evidence for widespread spatial synchrony in population fluctuations has been found in a variety of organisms (Paradis et al. 2000; Kendall et al. 2000), and some studies have found that weather is a likely candidate as a synchronizing factor (Paradis et al. 2000; Williams et al. 2003).

Climate per se is a major determinant of geographical distribution for many organisms and recent climate warming has been shown to affect the distribution of different species (Thomas and Lennon 1999; Parmesan et al. 1999; Hughes 2000). However, the potential impact of a change in environmental suitability on abundance within the range of a given species has received relatively little attention (Mehlman 1997; Williams et al. 2003). This is partly because there is generally little comprehensive information on the distribution of abundance within the range of a species and because long-term estimates of densities over wide geographic areas are uncommon (Williams et al. 2003).

In this paper, we study the pattern of population synchrony of three peripheral populations of the Lesser grey shrike *Lanius minor*, and the relationship between population fluctuations and weather. The Lesser grey shrike is highly endangered throughout Europe, having declined markedly in abundance and range in the last decades (Lefranc and Worfolk 1997). Relict populations of the species in the western limit of its breeding range are known to exist since long (Lefranc 1995). Such peripheral populations, now restricted to very small areas in southern France and northeast Spain, have been reported to decline in the last decades (Lefranc 1995; Giralt and Bota 2003, Giralt 2004). Overall, there is almost no information on which factors may be responsible for the general decline of the species (Lefranc and Worfolk 1997; Krištín et al. 2000). Some authors have pointed out loss of habitat (agricultural intensification) and adverse weather (Lefranc 1995, 1997; Lefranc and Worfolk 1997; Isenmann and Debout 2000) whereas others suggest that adverse circumstances on the wintering grounds or during migration may account for the decline (Herremans 1997a, 1998a). However, no specific work has investigated the causes underlying the decrease of the species. Whereas there is not much information on this shrike (but see Lefranc 1995; Herremans 1997a; Lefranc and Worfolk 1997; Isenmann et al. 2000; Krištín et al. 2000), the distribution of abundance of the species in its westernmost range and changes in the last decade are available, what provides a valuable opportunity for studying population fluctuations and general patterns of changes in abundance in response to environmental changes. Therefore we aim to: (i) evaluate the spatial scale of synchrony in fluctuations of several peripheral populations of this species, (ii) assess the role of climate on the decline of this shrike in an attempt to contribute to the conservation of this particular species. Additionally we aim to illustrate the challenges associated to the conservation of peripheral populations of endangered birds.

Methods

Study species and study area

The Lesser grey shrike is a socially monogamous long-distance migratory passerine whose breeding range is limited to warmer parts of Eurasia, spreading over 6,000 km from west to east (Cramp and Perrins 1993). The westernmost points reached by this species lie in southern France and northeast Spain (Lefranc and Worfolk 1997), at the farthest extreme of its migratory route. This shrike produces a single brood per season, although replacement clutches can be produced after nest failure. Birds arrive on the breeding grounds in Europe during May. In the study area the main egg-laying activity takes place from late May to early June and the main fledging period encompasses from late June to early July (Isenmann and Debout 2000; pers. obs.).

Two main breeding areas existed in Spain until recently (Giralt and Bota 2003). The breeding area in Girona (42° 16′ 42.84″ N 3°07′ 21.66″ E, Catalonia) lay in the Natural Park of Aiguamolls de l'Empordá (protected area since 1983) and its periphery, where the species bred for the last time in 2001 (Fig. 1). The breeding area in Lleida (Catalonia) is 220 km southwest from the first one, and consists of two nuclei 5,5 km apart from each other (Fig. 1). A third, relict nucleus remains in Aragón (35 km west of Lleida).

The breeding population of the study species in France is located in two main breeding areas, Montpellier (43°30′ 44.66″ N 3°39′ 15.26″ E, Hérault) (Isenmann et al. 2000) and Aude (43°15′ 53.48″ N 3°08′ 51.78″ E, departments of Aude and Hérault, Bara 1995), 60 km from each other and 180 and 120 km from the breeding nucleus in Girona, respectively (Fig. 1). Some isolated pairs (3 in 2002 and 1–2 in 2004) still breed in Vaunage (Gard) (Labouyrie 2003; pers. comm.).

The non-breeding range of the Lesser grey shrike is about one tenth of the size of its breeding range. During the non-breeding season, the world population concentrates in the southern African thornbelt, mainly in the Kalahari basin (Herremans 1997a, 1998a), spreading mostly over Botswana, Namibia and north of South Africa. Birds occupy their final non-breeding destination in January–March and almost all individuals have disappeared from the winter quarters by the end of April (Herremans 1997b).

Abundance data

Data on the past distribution of the species in the Iberian Peninsula have been collected from old and recent literature and personal communications. Long-term data on breeding population come from Girona where the population has been monitored during 1989–1997 (except 1992) by the staff of the Natural Park, and by D.G. from 1998 to 2004. Data on the current distribution of the species in Lleida have been collected on the basis of censuses performed by D.G. during the entire breeding season (15 May–10 July) for the period 2001–2004.

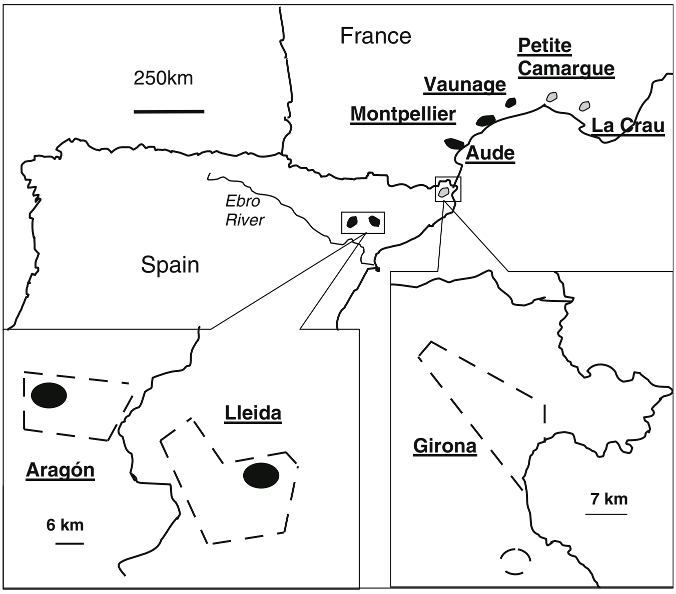

Fig. 1 Contraction of the breeding range of the French and Spanish populations of Lesser grey shrike. Current breeding areas (in black), past breeding locations (shaded areas) and contraction of the range (discontinuous lines) in the study areas are shown

Information about the two main areas in France was collected from Bara (1995), Isenmann et al. (2000), Donck and Bara (2001) and Rufray and Rousseau (2004) and kindly completed by Isenmann, Lefranc and Rufray. Censuses in the population in Aude started in 1992 (Bara 1995). The breeding population in Montpellier was discovered in 1995 (Béchet et al. 1995) and censused from that year onwards.

Abundance data from Spain and France are the result of censuses specifically undertaken to monitor the breeding population of this species. They were performed from territory establishment until fledging. Thus, such information reflects reliable actual counts.

Population trends, fluctuations and spatial synchrony

We studied the occurrence and intensity of population synchrony by correlating the fluctuations in the time series of the French and the Spanish (only Girona) populations (Paradis et al. 2000). We used the software program TRIM (Pannekoek and van Strien 2003), designed to analyze time series of counts with missing observations by using Poisson regressions, that produces estimates of yearly indices and trends.

First, we studied the trend of the French population (Aude and Montpellier) from 1993 to 2004 (two missing data—1993 and 1994—for the population in Montpellier) and of the population in Girona from 1993 to 2002 (although the species bred there for the last time in 2001 we assigned 1 pair to 2002 to allow a better comparison between both populations—see below). For these purposes we used a linear trend model with stepwise selection of change-points. Change-points are moments in time (i.e. years) where the slope parameter changes. This model provides an overall trend as well as selects specific time points (i.e. years) when the slope parameters differ significantly from the ones obtained before and after that time point. Possible violations to the assumption of Poisson distributions due to overdispersion or serial correlation were corrected with the methods implemented in TRIM.

Then, we explored whether the fluctuations of the Spanish (Girona) and French population (Aude and Montpellier) are interrelated by examining the relationship between the annual departures from the long-term trends of each population. For this we first calculated the trend for each population from 1993 to 2002 and the yearly deviations from each linear trend by using the time effects model implemented in TRIM. Since null values are not admitted when using the time effects model we restricted the study period until 2002 (breeding in Girona did not occur from 2002 onwards, see results), and considered one pair to breed in 2002 after checking that the linear trend obtained was similar to the one estimated with the linear trend model run with zero breeding pairs in 2002. In contrast to the linear trend model this one calculates separate parameters for each year and estimates yearly deviations from the linear trend. This model provides the best estimates for deviations of the general trend (van Strien, pers. comm.). Finally, we correlated the yearly deviations from the linear trends found in France and Girona.

Meteorological variables

We used meteorological data from the meteorological stations closest to each breeding population: Mauguio–Montpellier (Montpellier), Béziers (Aude) and Aiguamolls de l'Empordà (Girona), all of them less than 15 km from the respective breeding sites. Weather records consisted in daily rainfall (mm) during

January–July for the period 1989–2001 for Girona and maximum and minimum daily temperatures (°C) during May–June (encompassing most of the breeding period of the study species) for the period 1989–2002 for Aude, Montpellier and Girona. Daily thermal oscillation was calculated as the difference between the latter variables. Mean temperatures were calculated as the average of daily maximum and minimum temperatures.

Rainfall in Botswana and Namibia (October–February) was also gathered from the Tyndall Center for Climate Change Research (data set TYN CY 1.1, Mitchell et al. 2002). Since rainfall varies widely in and around the Kalahari we compared seasonal rainfall (October–February) during the years 1989–2000 with the mean rainfall for those months in the same areas for the larger period 1902–2000 (data set TYN CY 1.1). We got an average of 502.93 mm. We defined a threshold value of 150 mm below and above the long-term mean to classify years of the period 1989–2000 into ‘low’, ‘average’ and ‘high’ rainfall years (thresholds of 352.93 and 652.93 mm, respectively). Similar classifications have been applied in other studies (see, for instance, Wiegand et al. 1999, Tews and Jeltsch 2004).

Normalized difference vegetation index (NDVI)

The amount and vigor of vegetation at the land surface was estimated by means of the NDVI. This index, based on satellite images indicating the condition of rainfall-dependent vegetation in time, is strongly correlated with the fraction of photosynthetically active radiation absorbed by vegetation (see Asrar et al. 1984; Prince and Justine 1991; Myneni et al. 1997 for more details about the index and Sanz et al. 2003 for a similar use of the index).

NDVI data corrected by surface topography, land-cover type, presence of clouds and solar zenith angle were provided by Clark Labs in IDRISI format as world monthly images at spatial resolution of 0.1° in a 0–255 scale values. Using IDRISI32 software, we obtained mean NDVI values for the period May–June (at 1-month interval) from 1988 to 2000 for the square areas sized 0.25° occupied by breeding populations in Montpellier (E 3°30′–3°45′ N 43°25′–43°40′), Aude (E 3°–3°15′ N 43°10′–43°25′) and Girona (E 3°–3°15′ N 42°10′–42°25′) and for the period January–March (when most birds occupy their final wintering destination) from 1988 to 2000 for the wintering area (E 18°–28°, S 20°–27°). The selected wintering area matches the Kalahari basin defined by Herremans (1997a, 1998a) as the core area for the Lesser grey shrike.

Statistical analyses

Separate stepwise multiple regressions were performed to determine the effect of climatic variables (thermal oscillation) and NDVI indexes on the population size of each of the three peripheral areas. Thermal oscillations in the three study areas during May–June were the independent variables for the first set of analyses. For the second set we used the mean NDVI index during May–June of each study area as well as the mean NDVI index for January-March in the wintering grounds in Africa. Parametric tests were used where the assumptions for normality were met. In some cases transformations were used to meet the requirements for normality. Otherwise non-parametric tests were used. Statistical analyses were carried out with the

STATISTICA 6.0 package (StatSoft Inc. 2001). Unless otherwise stated means and standard errors are offered and two-tailed tests used.

Results

Contraction of the breeding range

The geographic range of the species at the southwestern limit of its distribution has contracted dramatically. The breeding nucleus in Girona, that held in 1989 around 50% of the estimated breeding population in Spain, contracted progressively until it became extinct in 2002 (Fig. 1). Although the breeding population in Lleida seems relatively stable during the last years (1.4, 2.4, 1.4 and 2.3 breeding pairs/km^2 for 2001–2004) the breeding range has contracted ca. 50% in last decade due to the progressive disappearance of breeding sites to the south and west of the current breeding area (Fig. 1). As a whole, the contraction of the range in Catalonia (Lleida and Girona) has been estimated at –68% between 1984 and 2002 (Giralt 2004).

The breeding area in Aragón, with ca. 2–7 pairs in the last 3 years, has also contracted during the last decade after disappearance of the easternmost breeding sites (Giralt and Bota 2003; Albero and Rivas, pers. comm.) (Fig. 1).

The French population has also declined in range due to the loss of breeding localities during the 90s in Gard (Petite Camargue) and Bouches du Rhône (La Crau), a stronghold of the species in the 70s (Lefranc 1999; Donck and Bara 2001; Labouyrie 2003) (Fig. 1). More recently, a 50% reduction of the number of pairs in the main nuclei (Aude and Montpellier) since 2002 (Rufray and Rousseau 2004) has contributed to the contraction of the range (Fig. 1).

Population trend and spatial synchrony in peripheral populations

Breeding populations of the Lesser grey shrike have been decimated along the southwestern range of its distribution (Fig. 2).

The decline of the species in France (Montpellier and Aude) fits a linear model (Likelihood ratio = 1.83, df = 10, $P = 0.99$) with a significant decreasing slope of 8.25% per year for the period 1993–2004 (Overall Multiplicative Slope imputed with intercept = 0.917, SE = 0.0069, $P < 0.05$). Particularly marked decreases in the trend occur between 1997–1998, 1999–2000, and 2001–2002 (Tables 1 and 3). During 2002–2004 there was a constant yearly decrease of 75% that has resulted in the lowest ever numbers of the French population (Fig. 2).

The decline of the Spanish population in Girona during the period 1993–2002 also fits a linear model (Likelihood ratio = 0.03, df = 1, $P = 0.85$) with a significant decreasing slope of around 14% per year for the period 1993–2002 (Overall Multiplicative Slope imputed with intercept = 0.856, SE = 0.013, $P < 0.05$) (Fig. 2). Similar to the French population, this tendency is not constant and several significant change-points can be distinguished (Table 2). Sharp decreases occur between 1993–1994, 1995–1996, and 1997–1998 whereas increases occurred between 1994–1995, 1996–1997 and 1998–1999 (Tables 2 and 3). During 1999–2001 there was a constant yearly decrease of 76% that, in fact, led to the extinction of the species in Girona from 2002 onwards (Table 3, Fig. 2).

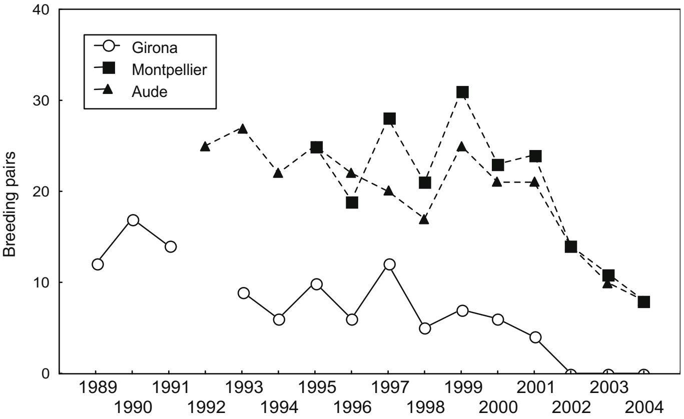

Fig. 2 Population trend of the Lesser grey shrike in Girona (Spain) (open circles) and two French populations (filled symbols) during the period 1989–2004

Table 1 Wald-tests for the significance between time-points of changes in the slope of the population trend of the Lesser grey shrike in France (Montpellier and Aude) during the period 1993–2004

Change-point	Wald-test	df	*P*
1993	2.80	1	0.09
1994	1.75	1	0.18
1995	2.64	1	0.10
1996	5.05	1	0.02
1997	6.29	1	0.01
1998	14.77	1	0.0001
1999	18.09	1	0.0000
2000	2.92	1	0.08
2001	9.59	1	0.002
2002	1.81	1	0.17

Annual deviations of the Spanish (Girona) and French population (Aude and Montpellier) from their respective long-term trends during 1993–2002 are strongly correlated (Pearson correlation, $r = 0.70$, $P = 0.024$, $n = 10$) (Fig. 3).

NDVI index and climate change in breeding and wintering grounds

The average of the mean temperature for May–June has not changed significantly in the period 1989–2002 in any of the studied locations (Girona, Aude, and Montpellier) (Pearson correlations, $P > 0.10$ and $n = 14$ for all cases). However, the average

Table 2 Wald-tests for the significance between time-points of changes in the slope of the population trend of the Lesser grey shrike in Girona (Spain) during the period 1993–2002

Change-point	Wald-test	df	*P*
1993	9.19	1	0.002
1994	14.59	1	0.0001
1995	21.38	1	0.0000
1996	26.11	1	0.0000
1997	52.98	1	0.0000
1998	24.20	1	0.0000
1999	11.64	1	0.0006
2001	14.91	1	0.0001

Table 3 Parameter estimates of the trend for each time interval (defined after significant change-points) referred to the French and Spanish population size in the previous interval

French population			Spanish population		
From–up to	Multiplicative slope	Standard error	From–up to	Multiplicative slope	Standard error
1993–1994	0.81	0.099	1993–1994	0.67	0.089
1994–1995	1.07	0.11	1994–1995	1.67	0.21
1995–1996	0.82	0.07	1995–1996	0.60	0.07
1996–1997	1.17	0.10	1996–1997	2.00	0.25
1997–1998	0.79	0.07	1997–1998	0.41	0.05
1998–1999	1.47	0.13	1998–1999	1.45	0.20
1999–2000	0.78	0.06	1999–2001	0.76	0.05
2000–2001	1.02	0.09			
2001–2002	0.62	0.06	2001–2002	0.23	0.06
2002–2004	0.75	0.05	–	–	–

thermal oscillation for the same season (May–June) and period has increased dramatically in Girona ($r = 0.90$, $P < 0.0001$) whereas there is no significant change either in Montpellier ($r = -0.39$, $P = 0.17$) or Aude ($r = -0.16$, $P = 0.58$). Precipitation (total amount during January–July) in Girona has not changed during 1989–2001 ($r = -0.30$, $P = 0.32$).

Climatic changes seem to have influenced the vegetation in Girona, where the mean NDVI index for May–June has decreased significantly during 1989–2000 ($r = -0.62$, $P = 0.033$, $n = 12$). We found non-significant negative correlations in the mean NDVI index for the same season (May–June) and period in the other study areas (Montpellier, $r = -0.16$; Aude, $r = -0.07$, $P > 0.50$ and $n = 12$ for all cases).

Overall, the NDVI index recorded during 1989–2000 for each area correlates with the one in the other areas (Pearson correlations, $P < 0.01$ in all cases).

An analysis of rainfall in the wintering grounds (October–February) during the period 1989–2000 suggests that it has not changed significantly ($r = 0.10$, $P = 0.76$, $n = 12$). A comparison of precipitations during October–February for each of the years in that period with the average precipitation (502.93 mm) and the threshold values (352.93 and 652.93 mm) (see Methods) for the longer series 1902–2000 suggests that only two seasons in the period 1989–2000 (1991/1992—273.1 mm—and 1994/1995—311.4 mm) can be classified as dry whereas the remaining seasons have average precipitations. Accordingly, the mean NDVI index for January-March does not show any trend along 1988–2000 ($r = 0.11$, $P = 0.72$, $n = 13$).

Population declines and climatic variables

Variation in the number of breeding pairs in Girona during the period 1989–2002 (except 1992) can be explained by climatic variables (i.e. thermal oscillation during May–June) in the local area. A multiple regression analysis provided a significant model (Table 4) where only thermal oscillation in Girona proved significant ($\beta = -0.92$, $P = 0.0007$), suggesting that the larger the thermal oscillation, the less birds in Girona (Table 4). Repeating the analysis with the NDVI values for the breeding locations and the wintering grounds (period 1989–2000) as independent variables yields a significant model (Table 4) where only the NDVI in Aude is excluded. The strongest effect was found for the NDVI in Girona

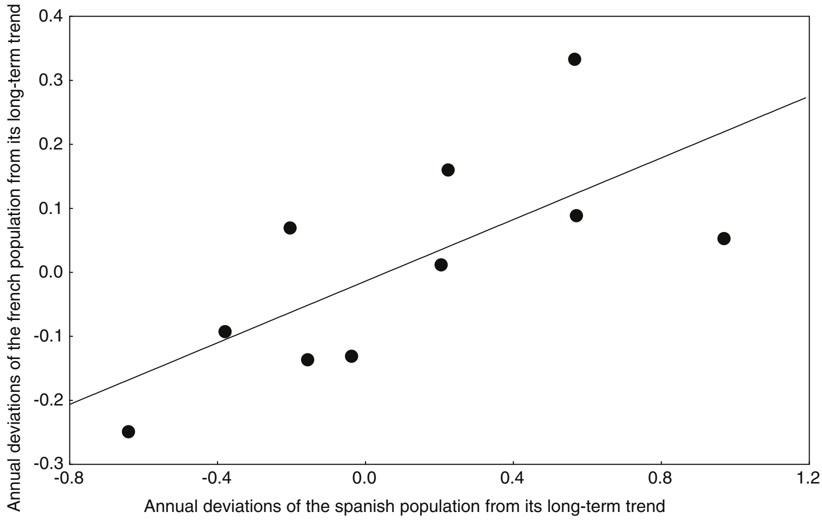

Fig. 3 Correlation between the annual deviations from the long-term trend calculated separately for the breeding populations of Lesser grey shrike in Girona (Spain) and France (Montpellier and Aude) from 1993 to 2002

(β = 1.44, P = 0.006), the other significant variables being the NDVI in Montpellier (β = –1.22, P = 0.009) and in the wintering grounds (β = –0.78, P = 0.01) (Table 4).

The fluctuations in the number of breeding pairs in Aude during the period 1992–2002 can be explained by a marginally significant model (P = 0.056, Table 4) where

Table 4 Results of stepwise multiple regression analyses with number of breeding Lesser grey shrike pairs in three peripheral populations (Girona, Aude and Montpellier) as dependent variables and (i) climatic variables (mean thermal oscillation during May–June), (ii) vegetation variables (mean NDVI index during May–June for the breeding locations and mean NDVI index during January–March for the wintering area) in each of these locations as independent ones. β coefficients, P values and statistics of each model are shown

Location	Thermal oscillation				Vegetation variables (NDVI)		
	β coeff.	P	Model		β coeff.	P	Model
Girona							
Girona	–0.92	<0.001	$F_{3,9} = 8.5$,	Girona	1.44	<0.01	$F_{3,7} = 6.3$,
Montpellier	–0.38	0.17	$P < 0.01$,	Montpellier	–1.22	<0.01	$P = 0.02$,
Aude	0.25	0.33	$R^2 = 0.74$	Wintering area	–0.78	0.01	$R^2 = 0.73$
Aude							
Girona	–0.71	<0.05	$F_{2,8} = 4.2$, $P = 0.056$,	Wintering area	–0.42	0.25	$F_{1,7} = 1.5$, $P = 0.25$,
Montpellier	0.29	0.28	$R^2 = 0.51$				$R^2 = 0.17$
Montpellier							
Montpellier	–0.39	0.33	$F_{1,6} = 1.1$, $P = 0.33$, $R^2 = 0.15$	No variable entered			

only thermal oscillation in Girona had a significant effect ($\beta = -0.71$, $P = 0.021$). Remarkably, thermal fluctuations in Aude did not enter the model. Variations in the breeding population in Aude during 1992–2000 could not be explained by the NDVI indexes in the breeding and wintering areas (non-significant model, Table 4).

Finally, we did not find any significant model explaining variation in the breeding population in Montpellier either with thermal oscillation (period 1995–2002, Table 4) or with NDVI indexes (period 1995–2000, no variable entered the model).

Discussion

Both the breeding range and the abundance of the Lesser grey shrike at the southwestern limit of its distribution have drastically decreased in the last decades. The French population has been decimated in a few years with a yearly decline of 8.25% during 1993–2004. A stronger yearly decline of 14% during 1993–2002 in the population in Girona resulted in the extirpation of the species from the northeast portion of its range in Spain. The extinction of the species in this protected area in 2002 seems durable and this may very well be the fate for the French population in the near future (Rufray and Rousseau 2004).

Several reasons have been argued to explain the decline of the Lesser grey shrike, most of them pointing out at large-scale processes (like agricultural intensification or climatic changes) acting on the breeding areas (Lefranc and Worfolk 1997; Isenmann and Debout 2000) or on the winter quarters (Herremans 1998a). However, to our knowledge, no specific study has been done in this regard. Our results show correlated fluctuations of the French and the Spanish population in the last decade (suggesting that their decline can be under the influence of a common factor) together with concomitant climate changes, what suggests that climate may play a role in the decline of the species (see Schaub et al. 2005). We found clear evidence of climatic change in our study area in Girona (a drastic increase in thermal oscillation during May–June) in the last years, what agrees with other studies performed in the area (Piñol et al. 1998; Peñuelas et al. 2002; Gordo et al. 2005). Specifically, Piñol et al. (1998) described an increase in temperature in northeastern Spain resulting from increased maximum but not minimum temperatures (1910–1994 period) or from the increase of both maximum and minimum temperatures (1968–1994 period). Such changes may have probably resulted in the observed decrease of the NDVI index in the area, which suggests less vigorous and abundant vegetation. For the two other study areas in France we found no significant trends either in climatic variables or vegetation index during the studied period (May–June). However, there is strong evidence supporting climate change in those areas too. Spring temperature (March–May) rose significantly at Montpellier during the period 1984–1992 (Chuine et al. 1998) and in this same area the flowering date occurred at progressively earlier dates during this period (Osborne et al. 2000).

Climatic conditions can directly influence survival and reproduction in birds (Ringsby et al. 2002 and references therein). Moreover, the peripheral location of these breeding populations could enhance the negative effect of climate change since density-independent factors, like weather, have a high influence on demographic rates in border areas (Hoffmann and Blows 1994; Mehlman 1997; Williams et al. 2003). Thus, it could be that shrikes at the border of the range are more sensitive to these changes than populations at the core of the area. In line with this, the only comparative data available come from a Slovak population, connected to the main breeding area, which keeps a stable and dense population since years (Kristín 1995; Kristín et al. 2000).

A non-mutually exclusive explanation is that climate changes may have altered the availability/quality of basic resources (like habitat quality or food abundance) that are known to largely influence the size of peripheral populations (McArdle et al. 1990; Williams et al. 2003). In fact, we found a positive relation between the breeding population in Girona and the NDVI index that, in turn, decreases with time. Alterations in northeast Spain in the last decades (like increased aridity—Piñol et al. 1998—or altered life cycles of plants and insects—Peñuelas et al. 2002) due to climatic changes may have resulted in a decrease of food availability and/or in a decoupling between bird physiology and their food supply (Crick et al. 1997; Visser et al. 1998; Sanz et al. 2003) that could influence the reproduction of this predator specialized on large phytophagous insects (Kristín 1995).

Alternatively, human-related activities could account for the decline of the species via habitat modification. Widespread agricultural intensification has been occurring in western Europe since the sixties. However, the protected area in Girona and its periphery has not experienced appreciable changes in the last decade (Romero and Martí, pers. comm.) and the breeding areas in France have not seemingly suffered substantial alteration so as to produce the observed drastic decline of the breeding population (Rufray and Rousseau 2004; Lefranc, pers. comm.).

Factors like drought or habitat changes on the wintering grounds could also account for the decline of the species (Herremans 1997a, 1998a). We did not find any significant trend in precipitation in the main wintering area, what agrees with previous findings (see Herremans 1998b and references therein). Whereas we did not detect differences in NDVI index either, qualitative changes in vegetation cover types in the Kalahari basin due to human and natural causes do have occurred (Ringrose et al. 2002), including an increasing prevalence of thorn trees and widespread bush encroachment. The Lesser grey shrike prefers in the wintering grounds open habitat with limited presence of trees, scattered low bushes and low grass cover that favors prey visibility (Herremans 1997a, 1998a). We found that increases in NDVI in Africa influenced negatively the breeding population in Girona. Thus, it is likely that human factors and/or a series of years with average precipitations could deteriorate the structural qualities of the habitat for the Lesser grey shrike (e.g. bush encroachment caused by overgrazing, increase of grass cover) and thus reduce food availability either directly or indirectly by reducing prey visibility (Herremans 1998a, b).

Our results have two remarkable aspects. One is the spatial synchrony of the studied populations, which can be caused by similar extrinsic effects operating on different populations (Kendall et al. 2000; Williams et al. 2003; Liebhold et al. 2004). Weather has been frequently reported as a likely synchronizing factor (Paradis et al. 2000; Williams et al. 2003). For the population in Girona we detected a strong relationship between climatic variables and fluctuations in population abundances. The lack of correlation for other populations can be due to inaccuracies of our climatic data (e.g. the period when temperature or any other environmental variable influences habitat quality could be different to the one here considered), to the interaction between climate and local factors (Ringsby et al. 2002) or to the limited sample size. However, both our results and evidence from other studies (Chuine et al. 1998, Osborne et al. 2000) suggest that the studied populations are under similar changing environmental conditions and, therefore, common climatic conditions could be one factor accounting for the observed population declines.

A second relevant aspect arising from our study is that the circumstances experimented by one population could influence the fate of neighboring populations. Variations in the population size of Aude are correlated with environmental variables in Girona. Similarly, the NDVI in Montpellier correlated negatively with the population size in Girona. The migration pattern of the species implies that birds have to pass through the breeding areas in France to reach the ones in Spain. It is therefore likely that these populations are closely interconnected, so that individuals produced in a population recruit into neighboring populations in the next breeding season. It could well be that some birds born in Spain could decide to breed in France the next year (philopatry in juveniles of this species is known to be low, Krištín et al. in press). On the other side, favorable conditions in, let's say, Montpellier, could influence birds' decision to stay there rather than continue on migration to Girona. Curnutt et al. (1996) showed that source-sink dynamics can explain variability at the periphery of a species range where population size is governed largely by migration rather than by reproduction and survival (Curnutt et al. 1996). The role of each of the studied populations in this dynamic remains to be investigated.

Conservation implications

Species with synchronous populations are thought to confront greater risk of extinction because density crashes can occur simultaneously in all populations (Heino et al. 1997; Palmqvist and Lundberg 1998). Faced to the widespread extinction of this species in the southwestern border of its range, it is crucial to identify the causes of the decline and the ecological mechanisms involved and to establish conservation measurements. Whereas the occurrence of a major factor accounting for the decline of this shrike would make its conservation easier, this is unlikely given its migratory nature and the variety of environmental conditions they have to face at different locations throughout the year (Schaub et al. 2005). Our study adds to the preservation of this species by identifying some issues of practical importance to conservation biology. The parallel fluctuations of the French and Spanish (Girona) populations suggest common causes for the decline of the species in this area. Our results suggest that climatic change, acting directly or indirectly on the different populations and probably moderated by local conditions (Osborne et al. 2000; Ringsby et al. 2002) can be one of such causes. However, the correlational nature of this study limits our ability to determine causal factors. More effort is needed to identify other possible factors and the exact mechanisms by which climate may influence population dynamics of this species so that mitigation activities can be implemented.

Although climate change can be observed globally, the magnitude of changes and their effects on organisms is likely to vary considerably within a given region (Osborne et al. 2000). It is therefore crucial to preserve those populations/areas where the study species seems to be stable (e.g. Lleida). However, conservation actions could prove useless if applied separately for some population given that the fates of these populations seem to be interconnected. In line with this more information is needed about the degree of interconnection among peripheral populations and between these and more central ones, and whether the spatial synchrony here reported occurs at a larger spatial scale.

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CAPÍTOL 2

Breeding at the border of the range: comparing peripheral and central populations to understand the decline of the Lesser grey Shrike (*Lanius minor*)

Nidificant al límit de l'àrea de distribució: comparant poblacions perifèriques i centrals per tal d'entendre el declivi de la trenca (*Lanius minor*)

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Nidificant al límit de l'àrea de distribució: comparant poblacions perifèriques i centrals per tal d'entendre el declivi de la trenca (*Lanius minor*)

David Giralt Jonama i Francisco Valera Hernández

RESUM: Les poblacions perifèriques i petites són propenses a experimentar diferents règims de selecció natural i són més sensibles als efectes de l'aïllament i de la deriva genètica que les poblacions centrals i grans. Per tant, la seva conservació planteja problemes específics, la resolució dels quals pot ser aconseguida, en part, mitjançant la identificació de variables clau través de la comparació de poblacions centrals i perifèriques. La trenca *Lanius minor* està en perill d'extinció a Europa, on algunes poblacions perifèriques encara romanen en el límit occidental de la seva àrea de nidificació (sud de França i el nord-est d'Espanya). En aquest treball s'ha estudiat la biologia reproductiva d'una població perifèrica i aïllada (nord-est d'Espanya) i s'han comparat els seus paràmetres reproductius amb els d'una població estable i densa (Eslovàquia) connectada a l'àrea de distribució principal de l'espècie. També s'ha analitzat l'abundància de depredadors i la distribució espacial dels nius en relació al resultats de la reproducció, per tal de posar en relleu els factors que poden explicar la disminució de la població espanyola. Els nostres resultats mostren que: i) la majoria dels paràmetres reproductius no diefereixen entre la població perifèrica i la central, amb l'excepció de la taxa d'envol, que va ser significativament menor en la primera, principalment a causa de l'alta mortalitat dels polls, ii) la depredació va ser la principal causa de el fracàs de cria en ambdues poblacions, amb valors similars, iii) la probabilitat de depredació de nius augmenta amb la proximitat de nius de garsa, iv) les agregacions de nius són més petites a la població perifèrica que a la central i el grau d'agregació no influeix en la depredació de nius, però té un efecte positiu per la taxa d'envol. Els nostres resultats suggereixen que factors locals (probablement la disponibilitat d'aliments i / o depredació) són responsables d'una baixa taxa denvol de polls podent contribuir, finalment, a la regressió de l'espècie a les poblacions perifèriques. Els esforços de conservació s'haurien de centrar en la comprensió dels factors que limiten la taxa d'envol i la formació de majors agregacions de parelles/nius i en la implementació de mesures que millorin el resultat reproductiu (per exemple, mitjançant la millora de la qualitat de l'hàbitat). És urgent elaborar programes de conservació abans que les poblacions existents siguin massa petites per atreure el reclutament d'exemplars.

Breeding at the border of the range: comparing peripheral and central populations to understand the decline of the Lesser grey shrike (*Lanius minor*)

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Abstract

Peripheral and small populations are likely to experience different regimes of natural selection and are more sensitive to the effects of isolation and genetic drift than non-peripheral and large populations. Thus, their conservation poses particular problems whose resolution can be partially accomplished by identifying key variables through comparison of central and peripheral populations. The Lesser Grey Shrike *Lanius minor* is highly endangered throughout Europe where peripheral populations still remain in the western limit of its breeding range (southern France and northeast Spain). Here we studied the breeding biology of a peripheral and isolated population (northeast Spain) and we compared its breeding parameters with the ones of a stable and dense population (Slovakia) connected to the main range of the species. We also analysed predator abundance and spatial nest distribution in relation to breeding performance in an attempt to highlight the factors explaining the decline of the Spanish, peripheral population. Our results showed that: i) most breeding parameters did not differ between the peripheral population and the central one with the exception of fledgling success, that was significantly lower in the former mainly due to high nestling mortality, ii) predation was the main cause of breeding failure in both populations, at a similar rate, iii) the probability of nest predation increased with proximity to magpie nests, iv) nest aggregations in the Spanish peripheral population were smaller than in central populations and did not influence nest predation but they did have a positive effect on fledgling success. Our results suggest that local factors (probably food availability and/or predation) are responsible of a low productivity that may finally result in the decline of the species at the border of its range. Conservation efforts should focus on the understanding of the factors limiting fledgling success and the formation of large nesting clumps and on the enhancement of breeding performance (e.g. by improving habitat quality). It is urgent to address conservation programs before the existing populations are too small to attract recruits.

Keywords: Breeding success, Breeding aggregations, Conservation, Geographic range, *Lanius minor*, Peripheral population, Predation.

Introduction

Geographically peripheral populations are often relatively small and isolated from central populations (Lawton 1993; Lesica and Allendorf 1995). They are likely to experience different regimes of natural selection than central ones since the relative importance of abiotic and biotic factors on distribution patterns and population limitation is liable to change according to the position within the geographical range (Randall 1982; Hoffmann and Blows 1994). Consequently, peripheral populations are more likely to be imperilled than central ones and a great deal of effort is frequently spent protecting such populations (Lesica and Allendorf 1995). Conservation of marginal populations requires a basic knowledge of the relative importance of local and general factors influencing such populations. Comparison of the demographic rates between the centre and the edge of a species range can provide such information as well as to increase our knowledge of conservation and management strategies (Randall 1982; Lawton 1993, 1996). Unfortunately, comparative reproductive or survival data from a number of populations of a given species in widely separated localities are relatively rare (García and Arroyo 2001).

The Lesser grey shrike *Lanius minor* is highly endangered throughout Europe, having declined markedly in abundance and range in the last decades (Lefranc and Worfolk 1997). Peripheral populations of this species still remain in the western limit of its breeding range (southern France and northern Spain) although in the last decade they have decreased dramatically (Lefranc 1995; Rufray and Rousseau 2004; Giralt and Valera 2007). The main suggested causes of decline for this species are general processes like loss of habitat (agricultural intensification) and adverse weather either on their breeding grounds (Lefranc 1995, 1997; Lefranc and Worfolk 1997; Isenmann and Debout 2000) or in their wintering quarters (Herremans 1998), although no specific work has been done with regard to the decline of this species (but see Giralt and Valera 2007). Nonetheless, local factors like predation (Krištín et al. 2000; Lovászi et al. 2000) or parasites (Valera et al. 2006) may also have important consequences for specific populations.

In this paper we attempt to ascertain the proximal causes of the decline of the Lesser grey shrike at its westernmost border of its breeding range by examining: i) the breeding parameters of the largest population in northeast Spain during five years, ii) the effect of predation on this population and its relationship with the most abundant nest predator in the area, the Magpie (*Pica pica*), iii) the occurrence of breeding aggregations (clusters) and its relationship with breeding parameters, and iv) the differences and similarities between the Spanish peripheral population and a stable and innermost population located in central Slovakia (Krištín et al. 2000). We discuss the conservation implications of our findings.

Methods

Study species and study area

The Lesser grey shrike is a socially monogamous long-distance migratory passerine whose breeding range is limited to warmer parts of Eurasia, spreading over 6000 km from west to east (Cramp and Perrins 1993). The westernmost points reached by this species lie in southern France and northeast Spain (Lefranc and Worfolk 1997), at the farthest extreme of its migratory route.

Two main breeding areas existed in northeast Spain until recently (Giralt and Bota 2003; Giralt and Valera 2007). The northernmost breeding area laid in Girona, near the France border, in the Natural Park of Aigüamolls (protected area since 1983) and its periphery. The other breeding area is located in Lleida, eastern of Ebro valley, 220 km southwest from the first one, and consists of two nuclei 5.5 km apart from each other. Shrikes of the first nucleus nest mainly on a linear forest along a channel (hereafter Channel) that separates irrigated cultures from dry ones. The second nucleus lies in a private property with irrigated cultures and linear forests along secondary channels and pathways (hereafter State). The subpopulation in Girona was surveyed during 1999-2001, when the species bred there for the last time, and data from this population were limited to breeding success and causes of nest failure. Both breeding nuclei in Lleida were intensively studied during the period 2001-2005 and data on breeding parameters, breeding success, causes of nest failure and breeding clumps were collected.

The population in Slovakia is not well within the breeding area of the species but it can be considered a central population since it is connected to the main breeding area and it is a permanent, stable and dense population (Krištín 1995; Krištín et al. 2000). Moreover, this is the only population for which accurate data on breeding parameters are published (Krištín et al. 2000; Hoi et al. 2004).

Breeding parameters

The study areas and their surroundings were daily scanned all over the breeding season (15 May-15 July) so as to find all the pairs and to map their nests. As a result, the whole Spanish breeding population, with the exception of some isolated pairs breeding in a small area 35 km far from Lleida (Aragón) (Giralt and Bota, 2003) was studied during the period 2001-2005.

To avoid disturbance to the breeding pairs, breeding parameters (laying date, clutch size, hatching success) were recorded with a camera (Ccd Sony 1/3" Super Had) attached to a pole and connected to a monitor. Most nests were monitored with this method once per 7-10 days. In some nests the date of clutch initiation was estimated by back-calculation, assuming that one egg was laid per day and that incubation lasted 15 days from the penultimate egg (Lefranc 1993). Breeding pairs were observed almost daily during the breeding period. When the adults were not recorded, we monitored the nest with the camera to check whether it had failed. If so, we climbed up the nest and scanned it and the ground around the nest tree, looking for the cause of nest failure. Nest failure due to unfavourable weather (mainly wind) was considered to occur when egg remains, dead nestlings or the nest were found on the ground after harsh climate. Given that nest desertion was infrequent (Krištín et al. 2000; pers. obs.) and losses due to human disturbance in our study area were very rare, empty nests during favourable weather were classified as predated. Partial losses were indirectly recorded as absent eggs/nestlings with respect to the initial clutch size/number of hatched eggs. Nests were closely observed around the calculated date of fledgling and fledgling success was therefore estimated on the basis of direct observations of the nestlings leaving the nest. We also report about the rate of breeding failure (i.e. nests where no chick fledged).

In 2003 we recorded juvenile survival by closely following familiar groups during a median period of 20.0 days (range: 14-29 days, *n* = 11 familiar groups) after chicks abandoned the nest. During this period the maximum distance between the family group and the nest averaged 968 m±188 (range 200-1875 m, *n* = 11). In 2004, almost half of nestlings (*n* =19) in the population were ringed and thus we could study juvenile survival by following the marked fledglings in the familiar groups until they left the study area.

Breeding clusters were considered to occur when the distance between neighbouring nests was less than 150 m because this distance (ca. 7 has around the nest) is the average territory size of the Lesser grey shrike (Lefranc 1993), where most of the hunting activity of the adults occur (Lefranc and Worfolk 1997; Wirtitsch et al. 2001; pers. obs.).

Predator abundance

The Magpie (*Pica pica*) was the most abundant potential nest predator in the study area. We estimated its abundance in Lleida during the breeding period of the Lesser grey shrike (May-July) with two methods. During 2001-2005 we used line transects (Bibby et al. 1992) to get a relative abundance index (IKA) of magpies. For each breeding nucleus, one 2 km-long transect was set on 2001 and 2002. In 2003-2005 we enlarged the transects (2.5 km in Channel and 2.8 km in State) and during 2003-2004 we set another one (1.7 km long) in Channel. Five-six censuses were performed along the transects during May-July and all heard and seen magpies were recorded. The second method to assess Magpie abundance was nest mapping. During April-May 2003-2005, active Magpie nests were georeferentiated and mapped on a 1x1 km grid map, and distances between them were then calculated with the Arcview GIS Version 3.1 (ESRI) package. Since a predator control program was run every year in State from 2003, thus causing Magpie nest failures and invalidating previously active mapped nests, we only used data on Magpie nest distribution from Channel.

Statistical analyses

To explore the relationship between Magpie abundance (IKA index) and predation of shrikes' nests we used the censuses done in June, when most cases of nest predation occurred (data of both transects in Channel during 2003 and 2004 were averaged). In this case we did use data from State since censuses did reflect the abundance of magpies regardless the occurrence of control programs or not.

We performed a logistic regression analysis with breeding success as the dependent binomial variable and distance (m) between Magpie and shrike nests as the predictor variable.

To compare the breeding parameters between populations (Spain vs Slovakia) we averaged yearly data so that the sampling unit for these analyses is year (data for the Slovak population come from Krištín et al. 2000). In contrast, when analysing breeding parameters for the Spanish population we pooled data (i.e. nests) from different years after testing for interannual variability. These two methods account for some small differences in the reported mean values (depending on whether the aim is to describe the Spanish population or to compare the Slovak and the Spanish populations). When comparing hatching failure among years and between populations we discarded two years with low sample size (*n* = 1), what accounts for differences in degrees of freedom among tests.

Parametric tests were used where the assumptions for normality were met. Otherwise non-parametric tests were used. Statistical analyses were carried out with the STATISTICA 6.0 package (StatSoft Inc. 2001). Unless otherwise stated, only first clutches are used and means and standard errors are offered.

Results

Breeding population, reproductive parameters and causes of failure in peripheral populations

The breeding population in Lleida in the last five years has kept relatively constant (averaging 16.6 pairs, range: 14-19) (Table 1) although breeding sites to the south and west of the current breeding area have disappeared in the previous 15 years (Giralt and Valera 2007). The breeding population in Girona, that held four pairs in 1998 and up to seven in 1999 became extinct in 2002 (Giralt and Valera 2007) after the failure of all breeding attempts in 2001.

Table 1.- Breeding population and breeding parameters of the Lesser grey shrike in Northern Spain from 2001 to 2005. Given are the means and standard errors except for laying date, for which median and ranges are offered. Sample sizes (number of nests) are in brackets.

	2001	2002	2003	2004	2005	Total
First clutches/ Replac. clutches	14 /1	19 /2	17/0	16 /2	15 /0	81 /5
Median laying date	2 June (19/5-10/6) (13)	31 May (20/5-7/6) (17)	27 May (19/5-12/6) (12)	29 May (21/5-8/6) (14)	1 Jun (23/5-8/6) (12)	31 May (19/5-12/6) (68)
Clutch size	5.6±0. 2 (5)	6.1±0.2 (12)	6.0±0.2 (12)	5.9±0.3 (8)	5.9±0.2 (9)	5.9±0.1 (46)
% Hatching failure	0.0 (1)	4.4±2.9 (7)	0.0 (1)	11.0±11.0 (3)	16.2±8.6 (6)	8.9±3.6 (18)
Nestling mortality (mean %/hatched nest)	26.4±9.7 (8)	30.9±9.7 (9)	19.7±1.5 (5)	4.9±3.1 (7)	12.5±7.9 (4)	20.4±3.9 (33)
Fledgling success (% of successful nests)	3.5±0.3 (13)	3.5±0.4 (13)	3.7±0.3 (12)	4.2±0.4 (11)	4.0±0.4 (8)	3.8±0.2 (57)
% Breeding failure of 1st clutches	14.3 (14)	31.6 (19)	29.4 (17)	33.4 (15)	40.0 (15)	30.0 (80)

During the study period there were no significant interannual differences in laying date (Kruskal-Wallis test, $H_{4,\,68} = 6.2$, $P = 0.19$), clutch size (ANOVA test, $F_{4,41} = 0.5$, $P = 0.71$), hatching failure ($H_{2,\,16} = 1.02$, $P = 0.60$), nestling mortality ($H_{4,\,33} = 6.7$, $P = 0.15$) , fledgling success ($F_{4, 52}$ = 0.7, *P* = 0.61) and breeding failure (L. regression χ^2 = 1.8, *P* = 0.17, df = 1) (Table 1).

Juvenile survival after fledging was high in our population. In 2003, on average 90% of the fledglings could be monitored in their respective familiar groups two weeks after leaving the nest (*n* = 11 familiar groups, range of juvenile survival per group: 60-100%). During 2004, 15 out of 19 ringed nestlings (79%) could be detected within the study area seven days after fledging and at least 14 birds (74%) were still alive 14 days after nest desertion.

Breeding failure was similar in Girona (47.0%, *n* = 17 nests from three years) and Lleida (30.0%, *n* = 80 nests from five years) (Proportion test, *P* > 0.05), but the main causes of failure differed between populations. Adverse weather was the first cause of breeding failure of first clutches in Girona (50.0%, *n* = eight lost nests from three years), this percentage being significantly different (Proportion test, *P* = 0.013) from the one recorded in Lleida (8.3%, *n* = 24 lost nests from five years). Predation was the main cause of failure of first clutches in Lleida (79.2%, *n* = 24 nests from five years) being significantly higher than in Girona (25.0%, *n* = eight nests from three years) (Proportion test, *P* = 0.009).

Comparing peripheral and central populations

There were no significant differences between the Spanish population and the Slovak one in clutch size (Mann-Whitney U test, U = 16.5, n = 5, 8, P = 0.60), the proportion of clutches with a maximum number of seven eggs (for Spain 17.4 %, n = 46; for Slovakia 8.6%, n = 107, Hoi et al. 2004; Proportion test, P = 0.11), hatching failure (Mann-Whitney U test, U = 2, n = 3, 2, P = 0.56) or complete breeding failure of first and replacement clutches (Mann-Whitney U test, U = 3.0, n = 7, 2, P = 0.24) (Table 2).

However, fledgling success was significantly lower in Spain than in Slovakia (U= 0.0, n = 5, 8, P = 0.003) (Figure 1) namely because, in contrast to the Slovak population, partial losses (mainly of nestlings) were frequent in Spain (Table 2). We registered losses during incubation (disappeared eggs) in four (15%) out of 26 nests (one egg lost in three clutches and two eggs in one clutch). Twenty (61%) out of 33 nests that were closely monitored during the chick-rearing phase lost at least one chick. The mean percentage of lost nestlings in relation to hatched eggs was 18.9%±4.7 (n = 5 years) (Table 2), the maximum value being 80% nestlings in one nest.

The relative importance of the causes of breeding failure was similar between the peripheral population in Lleida and the central population. Predation was the main cause of complete breeding failure in the Spanish population (average: 81.0%, *n* = five years) and in Slovakia (average: 54.7%, *n* = two years), the second most important one being unfavourable weather with 8.3% (*n* = five years) and 11.7% (*n* = two years) for Lleida and Slovakia respectively (Proportion test, *P* > 0.05 for both comparisons).

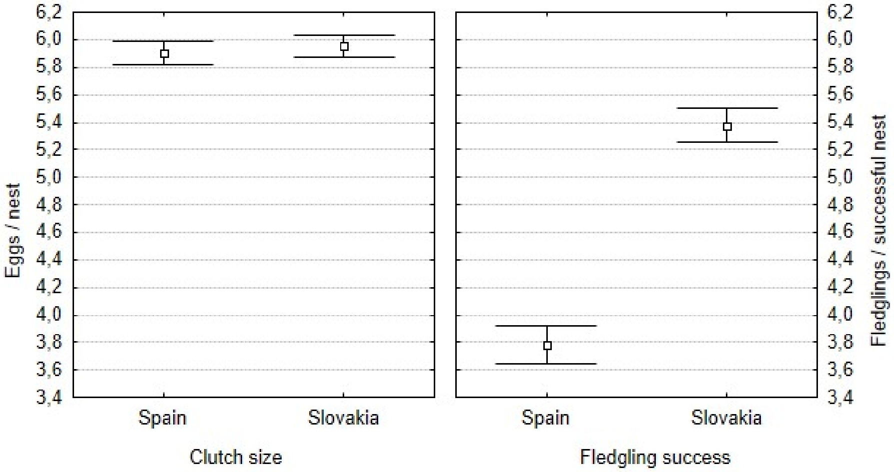

Figure 1.- Clutch size and fledgling success of the Lesser grey shrike in a peripheral (Lleida, Spain, this study) and a central (Slovakia, data from Krištín et al. 2000) population. Each empty point is a mean value for a given year and the major, filled symbols are the averaged means (SE are also offered).

Table 2. Breeding parameters of the Lesser grey shrike in a peripheral (Lleida, Spain, data from 2001 to 2005, this study) and a central population (Slovakia, data from Krištín et al. 2000). Average and standard errors of annual values are offered (number of years in brackets). Data on breeding failure include information collected during 1999 – 2001 in a second Spanish population (Girona). For correct comparison with data from Krištín et al. (2000), replacement clutches have been included when calculating breeding failure.

Breeding parameter	**Spain**	**Slovakia**
Clutch size	5.9±0.1 (5)	6.0±0.1(8)
Hatching failure (%)	10.5±3.4 (3)	8.2±1.4 (2)
Nestling mortality (%)	18.9±4.7 (5)	Insignificant
Fledging success	3.8±0.1 (5)	5.4±0.1 (8)
Breeding failure (%)	33.1%±3.0 (7)	26.0±5.0 (2)

Magpie abundance and predation

Breeding density of magpies in Lleida was high and averaged 12.3±0.1 nests/km^2 (*n* = three years, range: 10.8-14.3 nests/km^2) in April-May. We recorded a maximum of 23 nests in one 1x1km square in 2005. There was no correlation between the relative abundance of Magpies (IKA) and nest predation rate (first and replacement clutches pooled) (Pearson correlation, $r = -0.06$, $P = 0.87$, $n = 10$ locality-year cases).

However, at a lower spatial scale, the probability of predation on shrikes' nests was higher as the distance to the nearest Magpie nest decreased (Binomial Logistic Regression, $\chi^2 = 3.99$, $P = 0.046$, df = 1). The median distance to the nearest Magpie nest for predated (40.0 m, $n = 4$) and non-predated nests (117.5 m, $n = 10$) was marginally significant (Mann-Whitney U test, $U = 7.0$, $P = 0.066$).

Is conspecific nest aggregation advantageous?

The distribution of the distance to the nearest conspecific nest was non-normal in both breeding nuclei in Lleida (Kolmogorov-Smirnov test, Channel: $d = 0.27$, $P < 0.05$, $n = 36$, State: $d = 0.16$, $P < 0.05$, $n = 42$, data from five years pooled for both locations) as a consequence of a marked skew to short distances (Skewness = 1.8 and 1.9 for Channel and State respectively).

The distance to the nearest nest was marginally different between both nuclei (Mann-Whitney U test, $z = 1.71$, $P = 0.088$, $n = 36, 42$) (Median distance: State = 410 m, Channel = 152 m). In spite of this, we found a similar predation rate in each locality (State: 26%, $n = 42$; Channel = 22%, $n = 36$, pooling nests from all years).

Overall, the mean number of pairs/cluster in our study area was 2.2±0.2 (range: 2-4) ($n = 14$). Neither the percentage of predated nests (aggregated nests: 23%, $n = 30$, isolated nests: 25%, $n = 48$, Proportion test, $P = 0.84$) nor the percentage of nests with partial losses of nestlings (aggregated nests: 54%, $n = 13$, isolated nests: 65%, $n = 20$, Proportion test, $P = 0.52$) differed between aggregated and isolated nests. However, fledgling success of successful nests was significantly higher in aggregated nests than in isolated ones (mean and SE: 4.26±0.27 vs 3.53±0.20 respectively; t-test, $t = 2.2$, $P = 0.033$, $n = 19, 36$) (Figure 2). Whereas neither clutch size (mean and SE: aggregated nests: 5.95±0.13; isolated nests: 5.71±0.18; t-test, $t = 1.1$, $P = 0.27$, $n = 24, 24$) nor the percentage of nestling losses per successful clutch (mean and SE: aggregated nests: 15.2%±5.1; isolated nests: 23.8%±5.5; t-test: $t = 1.06$, $P = 0.29$, $n = 13, 20$), varied between both types of nests (Figure 2), the accumulated differences in both parameters probably account for the higher productivity of aggregated nests.

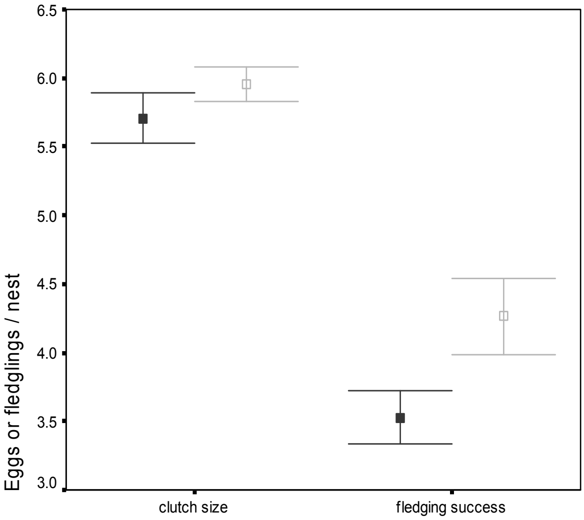

Figure 2.- Mean clutch size and fledging success for aggregated (grey) and solitary (black) pairs. Means, standard error are represented.

Discussion

Knowledge of population and reproductive parameters at the edge of species range may indicate the traits involved in limiting species abundance and distribution (García and Arroyo 2001). The low breeding density of the Lesser Grey Shrike in north Spain (1.8 nests/ km^2) (Giralt and Valera 2007), very similar to the one in the French peripheral population of Aude (1.7-1.9 nests/ km^2, Bara 1995) and much lower than in Slovakia (4.0 to 3.85 pairs/km^2, Krištín et al. 2000), was consistent with the decreased ability of individuals to thrive in peripheral areas (Lawton 1993). However, our comparison between the Spanish peripheral population and a stable, central one (see Krištín et al. 2000) evidences that most of the breeding parameters (including clutch size, hatching success and breeding failure) were quite similar in both locations. In contrast, fledgling success, one of the most important demographic parameters, was significantly lower in the Spanish population than in the Slovak one. Remarkably, this also seemed to be the case of the French population, where breeding failure was noticeably low (18.5%), but the average number of fledglings per successful nest was as low as 2.6 (Isenmann and Debout 2000). At least for the Spanish population, the low fledgling success was mainly due to the high rate of nestling losses (in 61% of nests some nestling disappeared), something very unusual in the Slovak population (Krištín et al., 2000). Since the first weeks of the juvenile period, a risky phase for many bird species including shrikes (see Yosef 1993), does not seem to be particularly risky in our study area, we conclude that the most critical phase in the breeding cycle of the Lesser grey shrike in our peripheral population (and probably in others like the French one) is the nestling stage.

Highlighting the causes of such a high rate of nestling losses is thus critical for the conservation of this species at the border of its range and for a better understanding of the importance of abiotic and biotic factors actually responsible in determining geographical range (Hoffmann and Blows 1994). The importance of abiotic factors (like adverse weather) on population limitation is likely to be higher at the border of the range than in central areas (Randall 1982). Weather was the first cause of breeding failure (50.0%) for the already disappeared subpopulation in Girona. Furthermore, some evidence suggests that climatic factors accounted for the long decline suffered by this population at least from 1989 until its extinction in 2002 (Giralt and Valera 2007). However, adverse weather did not seem to be a major limiting factor for the surviving population (Lleida, 8.3% of failed nests).

Biotic factors like predation or food availability are also likely to reduce the vital rates of organisms at the border of its range (Hoffman and Blows 1994). In fact, predation was the first cause of complete breeding failure in our population (ca. 80% of failed nests were predated), as well as in other breeding areas (Isenmann and Debout 2000; Lovászi et al. 2000). Furthermore, we found that the proximity of Magpie nests to shrike nests increased the likelihood of complete breeding failure for the latter, as it was demonstrated for this shrike in the Slovak population (Krištín et al. 2000) as well as for a closely related species (the Red-backed Shrike *Lanius collurio*) (Roos and Part 2004). Roos and Part (2004) also found that daily nest mortality rate (calculated from complete failures and partial losses) increased when shrikes bred inside Magpie territories, indicating that partial losses could be the result of predation activity of this corvid. In contrast, partial nest predation was rare in the Slovak population of Lesser grey shrike (Krištín et al., 2000), that had a similar predation pressure (55% of failed nests) than our population. Differences in breeding density and breeding aggregations between populations could probably account for this apparent disagreement.

The Lesser grey shrike usually forms breeding aggregations (Krištín et al. 2000 and references therein), probably as a consequence of conspecific attraction (see Etterson 2003 for the Loggerhead shrike *Lanius ludovicianus*). We did not find any effect of clustering in relation to nest predation rate, suggesting that nest aggregation is not an efficient mechanism against predation (see Krištín et al. 2000 for similar results). In contrast, Isenmann et al. (2000) found that clustered pairs in the French population suffered a lower nest failure rate, although they considered a larger distance (< 500 m to the nearest nest) to define a cluster. However, clustering did have a significant effect on fledgling success of Spanish population, since more chicks fledged in clustered nests than in isolated ones, what agrees with the results obtained by Valera et al. (2003) in the Slovak population. Thus clustering seems to be advantageous both for peripheral and central populations. Aggregations could be the result of habitat characteristics or the distribution of key resources (Etterson 2003; Lepley et al. 2004), which would mean that clusters are reflecting relative higher habitat quality patches than, in turn, could help adults to prevent partial predation via shared territory defence and/or nestling starvation (Reed and Dobson 1993; Hernández-Matías et al. 2003; Zanette et al. 2006). The lower cluster size in the Spanish population (aggregations in Slovakia were formed by up to 7 pairs, Hoi et al. 1997, while mean cluster size in Spain was 2.2 pairs/cluster) could account for the lower fledging success in our population as a result, for instance, of less efficient antipredatory defence. Alternatively, the formation of large breeding aggregations in peripheral areas could be precluded by the distribution/availability of basic resources (e.g. food, perches for hunting) that, in turn, would be reflected in a lower fledging success. Lepley et al. (2004) found different diet in aggregated and isolated Lesser grey shrike families. Preliminary results on the diet of this shrike in our area show that the mean prey size is smaller than the one found in Slovakia and that the richer habitats are scarcer in the peripheral population (in prep.). Thus, food shortage could also account for partial losses either directly and/or limiting the formation of large breeding clumps where partial predation is less likely (Hernández-Matías et al. 2003; Zanette et al. 2006).

Conservation implications

Our comparative results indicate that the main difference between a stable, central population of Lesser grey shrike and our declining, peripheral population is the low fledgling success caused by partial losses. Since past reproductive success of individuals influences breeding site fidelity (Switzer 1997, Haas 1998, Hoover 2003), a reduced fledgling success, together with factors probably operating during migration and wintering, will limit recruitment and the size of the breeding population in forthcoming years and the long-term viability of the peripheral population. The extinction of the breeding population in Girona after total failure of the decimated population in 2001 could be a good example. Hence, it is urgent to assess the role of the most suspected causes of nestling losses (partial predation and/or starvation) so as to enhance the fledgling success of the enduring populations by, for instance, providing food during the nestling phase (in prep.). Since breeding clusters result in a higher fledging success, probably reflecting the distribution of relative higher quality breeding areas (more food, less predators or a combination of both, Zanette et al. 2006), it is critical to exactly know the key habitat resources that limit the size of clusters in peripheral populations. Such knowledge is crucial to undertake management measures aimed to improve the habitat of this endangered species. In addition, return and survival rates for peripheral and central populations should be investigated, so as to definitely assess the future viability of the peripheral populations of the Lesser Grey Shrike in Western Europe.

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CAPÍTOL 3

The role of natural habitats in agricultural systems for bird conservation: the case of the threatened Lesser Grey Shrike

El paper dels hàbitats naturals per a la conservació dels ocells en medis agrícoles: el cas d'una espècie amenaçada com la trenca

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El paper dels hàbitats naturals per a la conservació dels ocells en medis agrícoles: el cas d’una espècie amenaçada com la trenca

David Giralt, Lluís Brotons, Francisco Valera i Anton Kristín

RESUM: Els ocells dels ambients agrícoles són un dels grups més amenaçats a Europa, a causa principalment de les seves tendències negatives en les últimes dècades. La intensificació agrícola derivada de l’aplicació de pràctiques dirigides a incrementar la productivitat agrícola, s'ha proposat com una de les principals causes d'aquestes regressions. No obstant això, especialment en algunes regions com a Europa de l’Est i a la Mediterrània oriental, es té poca informació sobre els factors últims lligats a la intensificació agrícola que han portat a la disminució d’aquestes poblacions d’ocells. La trenca és un bon cas d'estudi per a una millor comprensió d'aquests processos, ja que està estretament relacionada amb els hàbitats agrícoles i tant la seva àrea de distribució com les seves poblacions han sofert una forta regressió al llarg de tota la meitat occidental del continent. En aquest estudi, hem explorat les variacions en els paràmetres reproductius d'aquest lànid en relació a la composició de l'hàbitat i la disponibilitat d'aliment a escala del territori de nidificació. Hem trobat que la taxa d’envol de les parelles que nidifiquen més aviat està condicionada per la presència d’hàbitats naturals (matollars) i semi-naturals (guarets) en la matriu predominantment agrícola que domina els territoris de nidificació. La seva relació amb la taxa d’envol sembla estar relacionada amb una major disponibilitat d’artròpodes. De fet, les parelles de trenca mostren una marcada preferència per aquests hàbitats com a zones de cacera. Els nostres resultats posen de manifest la importància dels hàbitats naturals i semi-naturals en el mosaic agrícola, per a la conservació d'espècies dels ocells. Suggerim que els plans de gestió han de posar èmfasi en la disponibilitat d'hàbitats que serveixen com a reservoris d'aliment d'alta qualitat, contribuint a millorar la viabilitat de les poblacions d'espècies en aquestes àrees. Finalment, discutim la probable relació entre la intensificació agrícola i el declivi de les poblacions de trenca a Europa occidental.

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ORIGINAL PAPER

The role of natural habitats in agricultural systems for bird conservation: the case of the threatened Lesser Grey Shrike

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Abstract Birds of agricultural systems are one of the most threatened groups of birds in Europe mainly due to their sharp population decline in recent decades. Habitat intensification resulting from more productive agricultural practices has been proposed as a major cause for these declines. However, especially in some regions such as Eastern European and Mediterranean countries, little is known about the ultimate factors linked to habitat intensification that drive population declines for different species. The Lesser Grey Shrike is a good study species for a better understanding of such processes since it is closely related to agricultural habitats in Europe and has suffered a strong decline in range and population size across the western half of the continent. In this study, we explored variations in breeding parameters of this shrike related to habitat composition and food supply at the territory level. We found that fledgling success of early breeders was related to the presence of natural (shrub lands) and semi-natural (fallows) habitats in the predominantly agricultural matrix that dominated breeding territories. Their influence on fledgling success appeared to be mediated by a higher arthropod availability on these habitats. Indeed, Lesser Grey Shrike showed a strong preference for these habitats as hunting locations. Our results highlight the importance of natural habitats in intensified agricultural land mosaics for the conservation of bird species. We suggest that management plans should pay special attention to the availability of habitats which serve as high quality food reservoirs and can potentially contribute to enhance the species population viability in an area. Finally, we

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discuss the possible link between agricultural intensification and Lesser Grey Shrike population declines in Western Europe.

Keywords Agro-ecosystems · Arthropod availability · Biodiversity conservation · Fallows · Habitat selection · *Lanius* · Natural habitats · Reproductive success · Shrub-land

Introduction

Birds of farmland and grassland habitats have the worst conservation status in Europe (BirdLife International 2004). Estimates of population change available since 1970 indicate alarming declines, with 58% of these species undergoing significant decreases during 1990–2000 (BirdLife International 2004). These declines have been attributed to widespread deterioration and fragmentation of agricultural habitats across the continent (BirdLife International 2004). Intensification of agricultural practices, such as crop specialization, pesticide use and elimination of natural and semi-natural habitats such as margins or fallows have been proposed causes underlying the reported decreases in the quality of agricultural habitats (Tucker and Evans 1997). Although it is clear that no single mechanism is responsible, changes in agricultural practices over the last decades have been successfully related to the onset and the continuous tendency of bird population declines or range contraction (Fuller et al. 1995; Chamberlain et al. 2000; Donald et al. 2001; Benton et al. 2002).

The main mechanisms linked to agricultural habitat deterioration proposed to affect negatively bird dynamics through a combination of lower survival rate (Siriwardena et al. 1998) and reproductive output (Brickle et al. 2000; Siriwardena et al. 2000), have been: a reduction on food supply (Britschgi et al. 2006; Hart et al. 2006), the loss of key habitat features for nesting (Chamberlain et al. 1999; Browne et al. 2004) or foraging (Devereux et al. 2004; Butler et al. 2005) and direct mortality caused by specific farming practices (Crick et al. 1994; Corbacho et al. 1999). However, especially in some regions such as Eastern European and Mediterranean countries, we still ignore the ultimate demographic factors behind population changes for some conservation priority bird species (Donald et al. 2001; Newton 2004; Robinson et al. 2004).

Similar to other farmland birds, including shrikes, the populations of Lesser Grey Shrike have sharply declined and the species range contracted in Europe in the course of the last century, especially in the western half of the continent, from where it became extinct in many countries (Lefranc and Worfolk 1997). Threats for the species have been suggested to occur both in the breeding or winter quarters (Lefranc and Worfolk 1997; Herremans 1998), although there are more evidences supporting that causes acting during the breeding period have had a major role in population declines (see Lefranc and Worfolk 1997; Isenmann and Debout 2000; Giralt and Valera 2007). Agricultural intensification via the decrease in the abundance of large insect prey, as well as climatic processes, such as consecutive wet summers in central Europe leading to high rates of nest failure, have been suggested as important factors driving the population dynamics of this species (Krištín 1995; Lefranc 1995; Giralt and Valera 2007). As a result of the contraction and fragmentation of the western species range, small isolated populations remain now in areas of north eastern Spain and southern France, with less than 25 breeding pairs in each country (Giralt and Bota 2003; Rufray and Rousseau 2004; Giralt and Valera 2007).

The Lesser Grey Shrike occupies a variety of open habitat systems ranging form steppe, pseudo-steppe, grassland and farmland habitats, sparsely dotted with trees where it can build the nest. Territories include vineyards and fallows in France (Isenmann and Debout 2000), short-grass steppes in Hungary (Lovászi et al. 2000), meadows, orchards and bare ground in Slovakia (Wirtitsch et al. 2001) cereal and pasture in Italy (Guerrieri et al. 1995) and cereal, sparse shrub land and fallows in Spain (Giralt and Bota 2003). The wide variety of occupied land-uses across the range of the species suggests that some agricultural practices are compatible with the presence of the species as far as some key vegetation features (coverage of bare ground/herbaceous/shrub) and/or certain insect prey are maintained (Krištín 1995; Lefranc and Worfolk 1997; Isenmann and Debout 2000; Wirtitsch et al. 2001).

Many authors have paid attention to the scarcity of large arthropods as a key aspect behind the decline of the species in intensified agro-ecosystems in Central and Western Europe (Krištín 1995; Lefranc and Worfolk 1997; Isenmann and Debout 2000). Krištín (1995) found that food-niche width was relatively small when compared to the one of a related, ecologically very similar species such as the Red-backed Shrike (*Lanius collurio*), since the Lesser Grey Shrike relied on a narrower range of insects in relation to their body size (large prey items of 23 mm on average) and taxonomic group (feeding almost exclusively on *Coleoptera* and *Orthoptera*) (see also Cramp and Perrins 1993; Giralt et al. 2004; Hoi et al. 2004; Lepley et al. 2004). In spite of these disperse pieces of evidence on the importance of large insect prey availability and the presence of particular habitats or vegetation structures, there is a lack of detailed information about the mechanisms how these factors influence breeding the parameters of the Lesser Grey Shrike and may drive current population declines. In fact, the only study performed in this direction failed to find any relationship between habitat composition and breeding parameters (Wirtitsch et al. 2001).

In this paper, we aim to explore the potential relationship between food availability and habitat composition and use and their combined effects on the breeding performance of the Lesser Grey Shrike in a declining population at the south western border of its range. We hypothesise that food availability is a major criteria for shrikes' habitat selection and breeding performance and, thus, we predict: (i) habitat exploitation behaviour mediated by food abundance, and (ii) a direct relationship between habitat composition, food availability and breeding success. We focus on fledgling success (number of fledglings per successful nest) rather than on nest failure rate (failed nests in the population) given that the former was the only breeding parameter differing between the Spanish population and a healthy and stable population in Central Europe (own unpublished data, Krištín et al. 2000). The lower fledgling success in the Spanish population, caused by a high rate of partial losses of nestlings (23% of hatched eggs), is therefore probably liable for much of the decline in this region. Furthermore, we discuss to which degree the decline in western European populations may have been linked to the widespread loss of key habitats in the context of agriculture intensification. Because this shrike is always associated to partially or totally extensively managed agricultural habitats and appears to rely on the presence of large insects, it becomes a good study species to assess the effects of agricultural intensification process on farmland birds and biodiversity. In addition, given its unfavourable conservation status in Europe and its critical situation in isolated south western populations such as the Spanish one, our ultimate aim is to identify the key habitat features in order to develop adequate management aimed at stabilizing the remaining populations.

Study area and methods

Study species

The Lesser Grey Shrike is a long-distance migrant passerine that overwinters in the Kalahari basin, southern Africa, and breeds in warm, flat, open areas in Eurasia, extending from

Kazakhstan in the east to northern Spain in the west and reaching to 54–55° to the north in some areas of its distribution (Lefranc and Worfolk 1997). The breeding period typically extends from first days of May to mid July, laying taking place between the mid May and the first week of June. Incubation lasts 15–16 days and the nestling period normally between 16 and 18 days. Second clutches are not known, although replacement ones can be produced until the end of June. It is a monogamous and relatively gregarious species, breeding territories usually covering 6–8 hectares (Lefranc and Worflok 1997). Diet mainly consists of insects, particularly coleopterans and orthopterans, though sporadically can include vertebrates (Krištín 1995).

Study area and population

The Spanish Lesser Grey Shrike population is located at the Ebro basin, NE Spain, a flat area with a Mediterranean continental climate and only 300–400 mm of annual rainfall. The current population size is 20–25 pairs, divided in three small nuclei, two of them located 5 km far from each other and the third and smallest one, located 40 km away from the other two nuclei (Giralt and Bota 2003). Here we study one of these three nuclei that has been declining during the study period (2001–2005), holding 50% (7 out of 14 pairs) of the Spanish population in 2001 and only 15% (3 out of 15 pairs) in 2005. The study area is located along a 6 km long channel section where large trees are available for nesting. The channel separates dry cereal crops and natural and semi-natural habitats to the south from irrigated fruit trees to the north.

Foraging habitat selection

Foraging habitat selection was analysed for a total of 9 out of 26 breeding pairs (35%) in 2002–2004: 5 out of 11 pairs in 2002, 3 out of 8 in 2003 and 1 out of 7 in 2004. Several reasons account for this reduced sample size: (i) breeding failure precluded monitoring the foraging activity of eight pairs during the study period, (ii) four nests were located at the end of the breeding period and foraging activity could not be recorded, (iii) interannual overlapping territories with the same habitat composition, were not considered so as to avoid pseudo replication (five territories). Indeed, we only considered one repeated territory (2003–2004) since habitat composition differed markedly between years and, thus, we assumed that they were independent samples. Territory overlapping in the same year was observed for four pairs in 2002 but always represented less than 50% of the area of each plot (mean plot overlapping was 20.9 ± 8.3% SE, range 0–48.1%, $n = 9$).

We assessed habitat selection by comparing land use availability around each nest with the observed hunting areas of the respective adults. Land uses were mapped on a 1:5.000 scale at the start of the breeding period (second half of May) and updated at the beginning of June, after mowing and ploughing. Main habitats in the breeding area were crops, specifically dry cereal (barley and oats) and irrigated fruit-trees (apple and pear), while irrigated cereal occupied an insignificant area (see Results). Natural and semi-natural habitats were present and included shrub land (*Thymus vulgaris*, *Thymelea hirsuta*, etc.) and annual herbaceous fallows (*Sonchus oleraceus*, *Lolium rigidum*, etc.). Cereal fields were larger (2.58 ± 0.43 ha, $n = 10$ fields) than irrigated fruit-tree fields (0.26 ± 0.05 ha, $n = 10$), probably as a consequence of the lower economic profitability of the former, while natural and semi-natural patches had intermediate values in terms of size (1.74 ± 0.51 ha, $n = 8$). All habitats remained stable (no human management) during the whole shrike breeding period, except for the dry cereal which was mowed and often ploughed during the laying period, always before hunting activity data were collected. When ploughing occurred at that time of the season it was superficial still keeping cereal remains on the field. Thus we considered all stubbles in the same habitat category. Due to prevailing aridity of the study area, stubbles remained with low or very low plant cover (less than 15%) during the breeding period.

Whereas natural shrub-land and semi-natural fallow differed in dominant vegetation type (bush like in the first versus more herbaceous in the second), these two habitats keep meaningful similarities: (i) both had a null or very low degree of human management during the year, (ii) vegetation structure was very similar, with abundant patches of bare ground and sparse vegetation cover (<75% and very often between 25 and 50%, unpubl. data), (iii) the scarcity of precipitations (<400 mm of annual rainfall) and the hot spring and summer, precluded major seasonal changes in biomass, vegetation structure and floristic composition. Therefore, both habitat types were pooled in a single habitat category. In contrast to the surrounding cultivated land, shrub land and fallows showed a much higher degree of complexity in floristic composition, what is known to favour insect population density and stability (Morris 2000; Woodcock et al. 2007).

Land use availability was expressed as the percentage of area occupied by each habitat type in a 150 m radius plot centred on each nest. We considered this distance, equal to 7.1 ha, because it included most of the observed hunting events (69.5 ± 6.5% SE; $n = 9$ pairs) in our study area, as well as for other populations (Lefranc and Worfolk 1997; Wirtitsch et al. 2001; own unpublish. data). Moreover, in our study area habitat composition farther from the nests closely resembles the one within the plot here considered.

Foraging use of each pair was surveyed with binoculars and telescope along the breeding period and expressed as the percentage of ground hunting events in each habitat, which were recorded during adults' trips from nest to hunting areas. One hunting event was defined as every flight to the ground or to the air to catch a prey done by a perching bird. Observations for each pair were gathered in series of 1–2 h of intensive visual tracking distributed in 3–4 non-consecutive days. During each series of intensive tracking, hunting events were considered independent and thus included in the analysis, if they were recorded in different trips from the nest to the hunting area. A total of 290 ground chases and 47 aerial chases were recorded for nine pairs, which averaged 32.2 ± 3.8 (SE) and 5.2 ± 1.5 (SE) hunting events per pair respectively. Since aerial chases were frequently difficult to relate to a specific habitat type and since the frequency or such chases was low compared to ground ones (1:6), we focused foraging selection analysis on the latter. To assess habitat selection for each pair, we compared the percentage of area of each habitat type around nests (150 m nest-centred plots) with the observed percentage of ground hunting events in each habitat.

Arthropod availability

Arthropod availability was estimated in 2003 and 2004 using pitfall traps (Cooper and Whitmore 1990). Pitfall traps are commonly used to sample ground-dwelling insects such as *Coleoptera* but they are less frequently used for sampling *Orthoptera* because they can underestimate their abundance (Gardiner et al. 2005). However, as *Orthoptera* caches have been shown to be unaffected by habitat type and being mostly related to insect density and activity (Topping and Sunderland 1992), we assumed that any possible bias could occur at similar levels in all habitats, allowing us to compare relative biomass between them.

The traps were distributed throughout the four most common habitat types within the breeding territories: cereal stubbles, irrigated fruit trees, fallows and sparse shrub-land. We selected three fields of each habitat type, all of them inside the shrikes' territories. In each field we set four traps (10 cm of diameter) in a row 1.5 m apart from each other. All insects collected in each group of four traps per field were afterwards pooled and considered as our sampling unit. Thus, we obtained three sampling units (one per field) per habitat.

We sampled arthropod availability in two different periods (24 h each one): the first one between 1st and 3rd June, corresponding to the onset of Lesser Grey Shrike incubation period, and the second one between 30th June and 2nd July, corresponding to the second half of the nestling period. Thus, a total of three samples per four habitats, two periods and 2 years (=48 sampling units) had to be obtained, though pitfalls in two sampling points in 2004 were lost due to occasional sheep trampling, thus resulting in a final number of 46 sampling units.

Collected arthropods were preserved in 70% ethanol, identified in the laboratory at the family or genus level and assigned to a body length according to the most common size of each taxa. Only *Orthoptera* and *Coleoptera* larger than 10 mm were considered because they make up most of the diet of adult nestling shrikes (85–90% of prey items) (Krištín 1995; Giralt et al. 2004; Lepley et al. 2004). A total of 75 (year 2003) and 55 (year 2004) items were finally considered to calculate dry biomass (mg), on the basis of regression equations specifically performed for different families of insects (see Hódar 1996). Because we pooled different shaped and sized arthropods in the same analysis, biomass estimation should provide a more accurate picture of the occurring functional process than abundance (Saint-Germain et al. 2007). Therefore, arthropod availability is given as the dry biomass per sampling unit (four traps) and time (24 h.). Finally, given that Lesser Grey Shrike relies on the availability of large-bodied arthropods (Cramp and Perrins 1993; Krištín 1995) we separately estimated biomass for medium (11–20 mm) and large (>20 mm) sized items.

Effect of habitat types on fledgling success

We studied the relationship between habitat composition 150 m around the nest (area occupied by each habitat) and the number of fledglings produced by each pair (fledgling success). This analysis was performed for 22 breeding pairs, thus 61% of the studied population (2001–2005), from which the required information was available. We controlled for possible seasonal effects on clutch size or fledgling success by including hatching date in the analysis (Verhulst et al. 1995). Nests were checked during the breeding period (1–3 visits per nest) so as to provide accurate estimates of laying or hatching date. Fledgling success was obtained by counting the chicks with binoculars and telescope at the calculated fledgling date in order to minimise nest disturbance when fledglings were ready to fly.

We classified pairs in early and late breeders, considering their mean hatching date (17 June, $n = 22$). Mean hatching date of early and late breeders was 13 June (±0.7 SE, range: 9–16 June, $n = 11$) and 22 June (±1.3 SE, range: 17–30 June, $n = 11$) respectively. Then, we analysed the relationship between fledgling success and habitat composition and food availability for two different periods of the breeding season separately. In this way, any possible relationship between fledgling success and habitat composition could be better interpreted with data from our arthropod sampling periods, since the prevailing conditions for early breeders are best represented by our first sampling (all chicks of these pairs fledged before the second arthropod sampling) while the conditions experienced by late breeder are better represented by the second sampling.

Because our purpose was to study food-mediated habitat effect on fledgling success, we previously excluded from the analysis the failed pairs and one pair with only one fledgling, as we assumed that complete failure and heavy partial losses are probably more related to weather and predation than to food-mediated processes (Zanette et al. 2006). In addition, to avoid pseudo replication on habitat composition, one pair in 2002 was excluded as its plot overlapped more than 50% with a neighbouring one. The mean overlap between adjacent territories was 10.6 ± 4.1% (SE) (range 0–48.1%, *n* = 22). Thus, our study was finally performed with 65% (11 out of 17) and 58% (11 out of 19) of the early and late breeding pairs of the population during the study period (2001–2005). As no inter annual variation was detected in fledgling success for early (Kruskall–Wallis test, H = 1.792, d.f. = 3; *P* = 0.617) or late breeders (Kruskall-Wallis test, H = 0.049, d.f. = 2; *P* = 0.976) we pooled data from all the study period in the respective regression analyses. Given that hatching dates were not evenly distributed among years, it was necessary to ensure that the relationship between habitat and fledgling success was not an artifact due to a year effect. Preliminary analyses of the data showed that removing any possible year effect made no difference to the aforementioned relationship.

Statistical analyses

To assess habitat selection for each pair, Chi-square analyses were applied by comparing observed and expected percentages of hunting events in the different habitats. Expected percentages were obtained by multiplying the total hunting events by the relative area occupied by each habitat in the 150 m plots. Yates' correction for continuity was applied for the cases when only two habitats had been used to hunt (Zar 1999).

Arthropod biomass was log-transformed and analysed by means of general linear models (GLM, Type III Sum of Squares), considering habitat, year and period as fixed factors.

Finally, the potential relationship between fledging success and the available types of habitat was analysed by means of multiple regression analysis using a forward selection procedure. Previously, to ensure independence of the area covered by the three main habitats in the plots, we performed a Factor Analysis (Varimax rotation), extracting two factors that explained 95% of the variance of the original variables. The two resulting factors and hatching date were then used as predictors in the multiple regression analysis.

Means and standard errors are given in all analyses unless otherwise stated.

Results

Foraging habitat selection

The mean number of habitats in nest-centred plots was 3.4 ± 1.7 (range: 3–4) (*n* = 9) as plot composition was clearly dominated by cereal stubbles (38.2 ± 4.9%, *n* = 9), irrigated fruit trees (32.7 ± 3.9%, *n* = 9) and natural habitats (23.3 ± 4.8%, *n* = 9) (Fig. 1). Irrigated cereal was almost residual (4.0 ± 2.6%, *n* = 9) and the remnant 1.8% of the area corresponded to "others" category (buildings, woody areas, etc.).

The main habitat types for hunting was the natural ones (Fig. 1), where 71.0 ± 7.7% of the hunting events were recorded (*n* = 9). The other two available habitats were avoided but for different reasons. First, irrigated fruit trees, in spite of being extensively available for all pairs, were clearly ignored, as only 3 out of 290 chases from 2 out of 9 pairs were recorded in this habitat (and thus excluded from most chi-square analyses). Second, all pairs often used cereal stubbles as a hunting habitat (26.7 ± 8.3%, *n* = 9) but always below the expectations according to their availability in the landscape (Fig. 2).

Foraging habitat selection of early and late breeders followed the same pattern, both groups showing a clear preference for natural habitats and a negative selection for cereal stubbles and irrigated fruit-trees (Fig. 2). However, intensity of selection appeared to be

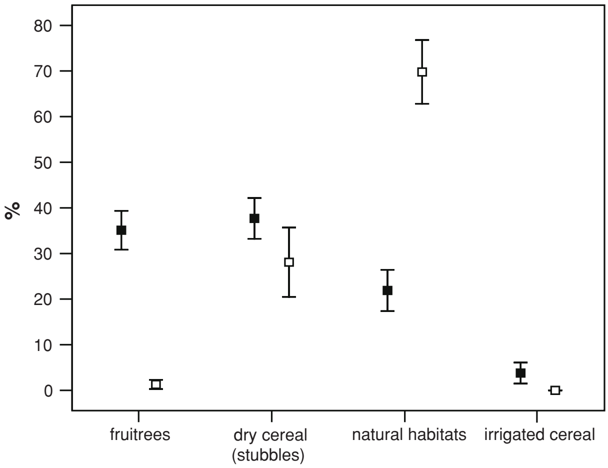

Fig. 1 Percentage of area occupied by the main habitat types on 150 m circular nest-centred plots (filled squares) and percentage of ground hunting events in each habitat (empty squares) ($n = 9$ territories). Mean percentages and standard errors are represented

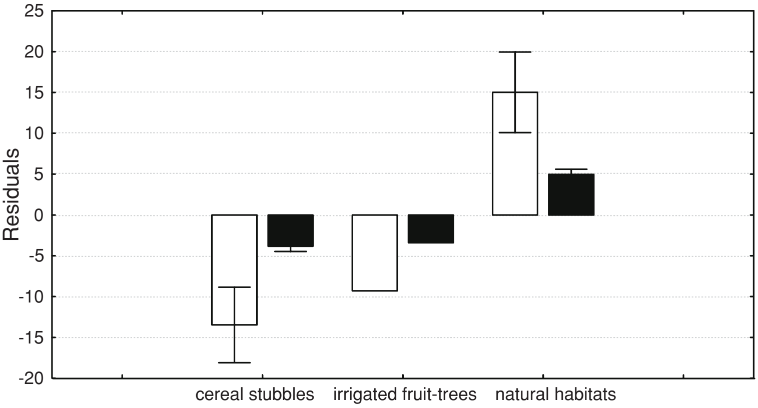

Fig. 2 Mean residuals of Chi square analyses for each foraging habitat type by early ($n = 6$) (stripped bars) and late ($n = 3$) (filled bars) breeders. Sample size in irrigated fruit-trees is one territory both for early and late breeders as this habitat had to be excluded from most of the analyses. Means and standard errors are represented

higher in early than in late breeders, as it is reflected by the higher absolute values of residuals in the former (Fig. 2). Finally, aerial chases ($n = 47$ observed in the nine pairs) showed a similar pattern than ground chases: 40% were performed within natural habitats, 19% in cereal stubbles and 0% in irrigated fruit-trees (the remnant 41% of aerial chases could not be attributed to a single habitat type).

Arthropod availability in the habitats

A total dry biomass of 16,003 mg of medium sized (11–20 mm) and large sized (>20 mm) orthopterans and coleopterans was collected during 2003 and 2004, corresponding

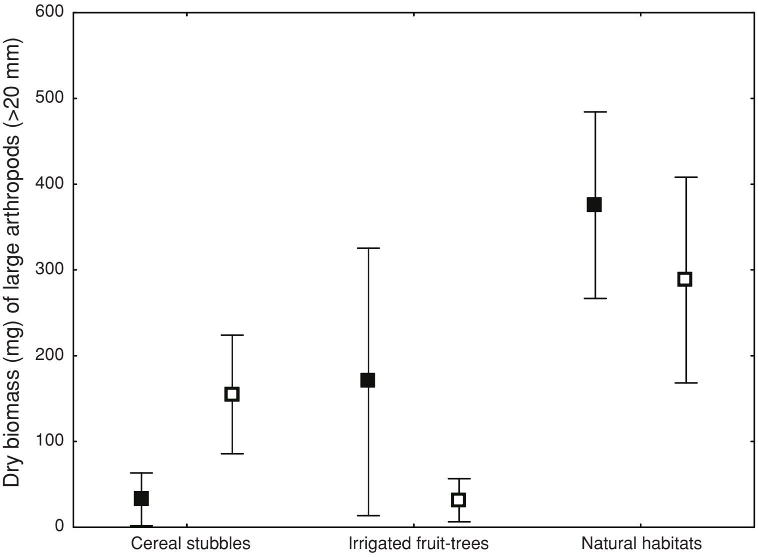

Fig. 3 Dry biomass (mg) of large arthropods (>20 mm) by habitat and period (filed and empty squares correspond to the first and second sampling period respectively). Means and standard errors are represented

basically to three families: *Tenebrionidae* (*Coleoptera*) 32%, *Gryllidae* (*Orthoptera*) 28%, and *Carabidae* (*Coleoptera*) 20%. A mean dry biomass of 397.5 ± 104.3 mg ($n = 24$ sampling units) and 293.8 ± 68.4 mg ($n = 22$) was collected in 2003 and 2004 respectively. Per habitats, mean biomass per sampling point was 463.1 ± 102.5 mg ($n = 24$) in natural habitats, 340.7 ± 87.8 mg ($n = 10$) in cereal and 123.5 ± 81.2 mg ($n = 12$) in irrigated fruit-trees. Mean dry biomass at the start and at the end of the breeding season was 401.9 ± 103.5 mg ($n = 23$) and 293.9 ± 73.5 mg ($n = 23$) respectively.

Large arthropod (>20 mm) biomass variability was partially explained by the habitat factor (Table 1) (GLM, Habitat: $F = 3.33$, $P = 0.04$, d.f. = 2), natural habitats supporting two to three times higher biomass than irrigated fruit-trees and cereal stubbles (Fig. 3). These differences tended to be more pronounced at the start than at the end of the breeding season, although the large variability observed probably hindered significance of the interaction effect (GLM, habitat*period: $F = 2.5$, $P = 0.09$, d.f. = 2). Dry biomass variability of medium sized insects (11–20 mm) was not explained by any of the considered variables (Table 1), although cereal stubbles tended to have higher medium-sized insect availability in 2004 (GLM, habitat*year interaction $F = 2.81$, $P = 0.07$, d.f. = 2).

Effect of habitat on fledgling success

Mean fledgling success was 4.3 ± 0.2 (range 2–7) fledglings/pair ($n = 22$), being higher for early (4.8 ± 0.2, range 4–6, $n = 11$) than for late breeders (3.8 ± 0.4, range 2–5, $n = 11$) (Welch test, $t = 6.37$; d.f. = 1,14.9; $P = 0.023$).

The three main habitats present around the nests were summarized in two factors explaining 95% of the total variance in the original variables (Table 2): the first factor ("human management") explained 62% of the variance and included natural habitats and cereal stubbles, and thus was related to a gradient from cropped (negative values) to abandoned

Table 1 Effects of habitat type, year and period on log10 of arthropod biomass (mg) (GLM type III)

Dependent variable	Effect	Sum of squares	df	*F*	*P*
Log arthropod >20 mm	Habitat	9.79	2	3.33	0.047*
	Year	0.05	1	0.04	0.850
	Period	0.05	1	0.03	0.856
	Habitat*Year	1.59	2	0.54	0.587
	Habitat*Period	7.34	2	2.51	0.095
	Habitat*Period*Year	0.58	2	0.20	0.823
	Error	51.42	35		
Log arthropod 11–20 mm	Habitat	7.07	2	2.62	0.087
	Year	0.64	1	0.47	0.497
	Period	0.00	1	0.00	0.983
	Habitat*Year	7.59	2	2.81	0.074
	Habitat*Period	3.19	2	1.18	0.319
	Habitat*Period*Year	0.59	2	0.22	0.804
	Error	47.26	35		

Table 2 Factor analysis of the three main available habitat types in 150 m nest-centred plots (Varimax rotation)

Original variables	Factor 1	Factor 2
Cereal stubbles	−0.869	−0.412
Irrigated fruit-trees	0.071	0.988
Natural habitats	0.967	−0.100
Explained variance R^2	62%	33%

Table 3 Effect of parameters related to habitat composition (factor 1 = human management, factor 2 = irrigated cultures) and hatching date on fledgling success (no. of fledglings/successful pairs) of early Lesser Grey Shrike breeders ($n = 11$)

Variables	Beta coefficient	*P*	Model
Constant	4.879	0.000	$F = 16.83$, $P = 0.003$, $R^2 = 0.61$
Factor 1	0.608	0.003	
Factor 2	−0.071	n.s	
Hatching date	0.016	n.s	

or less managed areas (positive values). The second factor (33% of the variance) included the extension of irrigated fruit-trees and thus provided information about the presence of irrigated land around shrike nests.

A forward multiple regression analysis provided a significant model ($F = 16.8$, d.f. = 10; $P = 0.003$) with the "human management" factor explaining 61% of fledgling success variability of early breeders ($t = 4.1$, $P = 0.003$) (Table 3). Indeed, the area occupied by natural habitats around nests was positively correlated with fledgling success of early breeders (Pearson correlation, $r = 0.79$, $P = 0.004$, $n = 11$) (Fig. 4). Although the mean area occupied by natural habitats around nests was similar for early (1.4 ± 0.2 ha, $n = 11$) and late (1.7 ± 0.3 ha, $n = 11$) breeders (Welch test, $t = 0.63$; d.f. = 1,16.5; $P = 0.44$), this positive effect did not arise for late breeders (no significant model was found), whose clutches hatched on average 9 days later (13 June vs. 22 June). Furthermore, the "irrigated cultures" factor had no effect on fledgling success of early or late breeders.

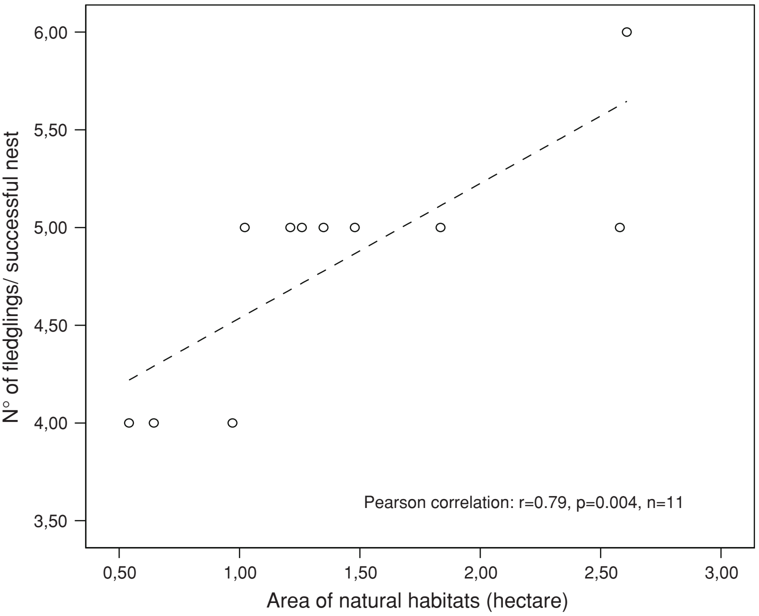

Fig. 4 Correlation between fledgling success of early Lesser Grey Shrike breeders and availability of natural habitats (hectare) at the 150 m nest-centred plots

Discussion

Habitat selection mediated by arthropod availability

Adult Lesser Grey Shrikes did not hunt at random within their breeding territories; rather they showed a clear habitat selection pattern both for early and late breeders. First, permanent natural areas proved to be the key habitat during foraging since they received 70% of total hunting events, much more than expected by the availability of this habitat (Figs. 1, 2). Second, even though cereal stubbles were visited by shrikes (about 25% of hunting events) they were used less than expected from their availability. Finally, irrigated fruit-trees were clearly avoided as less than 1% of the hunting events were recorded in this habitat. Percentage of aerial chases showed the same pattern of habitat usage than ground chases, thus confirming that habitat selection was independent of the displayed hunting technique.

This pattern of selection was congruent with among-habitat differences in large arthropod (>20 mm) abundance measured by means of dry biomass (Fig. 3). Natural habitats had two to three times more biomass of large insects than the other habitats. Therefore, a higher probability to find large orthopterans and coleopterans in every hunting trip would be determinant in the foraging habitat selection pattern shown by adult shrikes in the breeding territories. A trend for a reduced difference between habitats in arthropod availability at the end of the nestling period existed, although a larger sample size would be needed to confirm this seasonal effect (Fig. 3). On the other hand, abundance variability of medium sized insects (11–20 mm) could neither be attributed to the habitat type nor to the sampling period and year (Table 1).

Apart from insect abundance, other factors such as vegetation cover or perch availability and thus, prey access, can play a complementary role on foraging habitat selection as it has been demonstrated for shrikes and other “sit & wait” predators (Stephens and Krebs 1986; Yosef and Grubb 1994). In this sense, Wirtitsch et al. (2001) found in a stable and dense, slovak Lesser Grey Shrike population located in a traditionally managed agrosystem with high arthropod abundance, that mowed meadows and bare ground were the key habitats for hunting, as their lower plant cover offered higher prey access to shrikes. In southern France, the Lesser Grey Shrike population seemed to profit from ecotones of rich-food habitats (fallows) and low vegetation cover areas (vineyards), although foraging selection and arthropod availability was not directly analysed (Isenmann and Debout 2000). Although we did not assess prey access, plant cover did not seem to be a limiting factor in our arid study area (less than 400 mm of annual rainfall), since all habitats offered patches of bare ground (pers. obs.). Thus, in contrast to the Slovak population, for Spanish birds, the presence of natural habitats with large insect abundance appeared to be a key aspect in foraging selection, probably as a result of a higher degree of agriculture intensification in cropland habitats: for example, 37% of the area around shrikes’ nests was occupied by fruit-trees, which were continuously sprayed with pesticides during the whole Lesser Grey Shrike breeding period because of the high risk to develop fungal and insect pathologies (spraying was very rare in the study area of the Slovak population, pers. obs.). Effectively, considering total biomass of medium and big arthropods, irrigated fruit trees was the poorest habitat in terms of food resources. With reference to cereal crops, the second most abundant habitat in our study area, mowing and very often ploughing occurred just at the start of the breeding season. This agricultural practice is known to negatively affect insect availability, especially of larger insects (Beintema et al. 1991).

Effect of natural habitats on reproductive output

Concerning early breeders, our results support the prediction that fledgling success is favoured by the availability of rich-food hunting habitats. We found that the number of fledglings produced early in the season by a successful pair was positively related to the extension of natural habitats in the 150 m nest-centred plots (Table 3, Fig. 4). Furthermore, cereal stubbles as well as irrigated-fruit trees had no significant effect on reproductive output, which was in accordance with the fact that they were negatively selected during hunting trips and that they held lower availability of large insects. In the context of central place foraging theory (Orians and Pearson 1979) and considering that the Lesser Grey Shrike is a single-prey loader (Krištín 1995), we thus suggest that higher availability of large arthropods in natural habitats allows shrikes to improve their energy trade off during hunting activity, bringing more food per trip to chicks and thus minimizing nestling mortality (Sejberg et al. 2000; Redpath et al. 2006).

However, the reproductive output of late-breeders was not seemingly affected by habitat composition at the territory level. This is remarkable because late breeders still preferred to hunt on natural habitats (Fig. 2) and these pairs showed a non significant trend to occupy territories with higher availability of natural habitats (1.7 ha vs. 1.4 ha). In addition, we detected a marginal seasonal trend for large insects to decrease in abundance in natural habitats (Fig. 3), which could account for the lack of relationship and could be give sense to the observed lower fledgling success of late breeders. This temporal food decrease should be confirmed in further studies, since foraging behaviour indicated that no other habitat could replace natural habitats as a food source for chicks. Although natural habitats continued to be the main food-reservoir of large insects at the end of the season, such decrease could lead insect availability below a certain threshold, insufficient to avoid nestling starvation or to allow us to detect a positive effect of this habitat on fledgling success. Finally, considering that we just detected a non significant prey biomass decrease of 25% across the season in natural habitats (Fig. 3), we cannot reject the existence of other major factors that could hinder the importance of territory habitat composition and prey availability for late-breeders. Although beyond the aim of this study, we suggest that predator processes (Zanette et al. 2006; Rastogy et al. 2006) or reproductive constraints imposed by the short breeding season and long-distance migratory behaviour (Siikamaki 1998; Hemborg et al. 2001) of this species, could be more essential for the reproductive output of late-breeders than habitat composition.

Conservation implications

Fragmentation and loss of uncultivated or non-crop habitats, such as open shrub land and fallows, has been a common process in the increasingly intensified agricultural ecosystems across Europe in the last century, parallel to the decrease of many agricultural birds (BirdLife International 2004). As it has been described for the whole Iberian peninsula (De Juana et al. 1988), in our study area sparse shrub land has been progressively replaced during the last century by crops with the help of more powerful tractors and with the aim to increase crop production, while fallows have become much less essential due to a greater availability of fertilizers coming from pig livestock (Suárez et al. 1996). Here we find that these habitats, which are rapidly disappearing in current European agricultural landscapes, have a positive effect on fledgling success of at least a fraction of the Lesser Grey Shrike population (early breeders), because they provide higher resource availability, specifically through a higher abundance of large orthopterans and coleopterans. According to our results, at least 1.5 hectares of natural habitats at a maximum distance of 150 m from the nest (thus at least 20% of the surrounding area) should be necessary for a pair to produce five fledglings (Fig. 4), which is supposed to be the actual threshold for the viability of Spanish population (unpublished data). As natural habitats should represent more than 20% of the area in the surroundings of the Lesser Grey Shrike breeding territory to ensure the aforementioned productivity and population viability, we suggest to apply the same percentage at a landscape level in breeding sites where intensive nest search is not viable. Therefore, these habitats, which function as food reservoirs in intensified agricultural ecosystems improving Lesser Grey Shrike reproductive output and population viability, should be maintained and specially favoured at the territory and landscape level when developing and applying management plans. In fact, the presence of these habitats is often pointed out as an important requirement for the conservation of many other farmland birds in Europe (Tucker and Evans 1997; Brickle et al. 2000; Soderstrom et al. 2001). Nevertheless, we have found evidences that a seasonal reduction of large prey could be limiting the reproductive output of late breeders in our study population. Thus, further research is needed to identify and neutralize through management actions the factors that are limiting their breeding performance, as a way to increase their contribution to the overall reproductive success of the population.

To our knowledge, this is the first time for the endangered Lesser Grey Shrike that some habitat feature has been successfully linked to such an important demographic parameter (fledgling success). Thus, though very likely not the only one, we have identified an important mechanism linking habitat deterioration, resource availability and reproductive output. Despite the small population size from where these conclusions are extracted, it seems therefore feasible, as other authors have suggested (Krištín 1995; Lefranc and Worfolk 1997), that the species decline across Europe during the second half of the last century could be partly related to the process of substitution of natural and semi-natural habitats (margins, shrub land, fallows, pastures, etc.) by intensified crop monocultures. In the countries of EU 15, this process has been more pronounced in continental Europe than in Mediterranean areas (Donald et al. 2001), paralleling the extinction and fragmentation pattern of west European Lesser Grey Shrike populations: extinction in the north (e.g. northern France, Germany, Belgium) but small populations still existing in the south (Spain, south France and Italy). Due to the unfavourable conservation status of the Lesser Grey Shrike, it would be a priority for these remnant Mediterranean populations to detect and favour the key habitats that function as arthropod prey reservoirs. Finally, the same should be considered in eastern European countries that have recently joined the EU, such as Romania and Bulgaria, where the Lesser Grey Shrike has its last European strongholds.

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CAPÍTOL 4

Population decline is accompanied by loss of genetic diversity in the Lesser Grey Shrike *Lanius minor*

El declivi poblacional va acompanyat d'una pèrdua de la diversitat genètica en el cas de la trenca *Lanius minor*

Kvist, L., Giralt, D., Valera, F., Hoi, H. Kristin, A., Darchiashvili, G., & Lovaszi, P., 2011. Population decline is accompanied by loss of genetic diversity in the Lesser Grey Shrike Lanius minor. Ibis, 153: 98-109.

El declivi poblacional va acompanyat d'una pèrdua de la diversitat genètica en el cas de la trenca *Lanius minor*

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RESUM: La trenca ha patit descensos poblacionals successius i una marcada contracció de la seva àrea de nidificació des del segle XX, en gran part a causa de la intensificació agrícola. Això ha donat lloc a una distribució molt fragmentada a Europa Occidental, amb nuclis de nidificació aïllats a Espanya, França i Itàlia, i una distribució més contínua a Europa de l'Est i Àsia. A partir d'una combinació de marcadors nuclears i mitocondrials, s'ha avaluat l'estructura i diversitat genètica de diferents poblacions de Trenca des de l'Europa Occidental, passant per Europa Central i fins a Àsia. S'observa una diferenciació genètica significativa entre tres grans grups, un a Europa i dos a Àsia. La diversitat genètica és menor en la població espanyola, la més petita i marginal. Aquesta limitada diversitat genètica, combinada amb el ràpid descens poblacional, suggereix que la població espanyola pot estar enfrontant-se a l'extinció en un futur molt proper.

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Population decline is accompanied by loss of genetic diversity in the Lesser Grey Shrike *Lanius minor*

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The Lesser Grey Shrike has suffered successive declines in population size and a marked contraction of its breeding range since the early 20th century, largely because of long-term agricultural intensification. This has resulted in a severely fragmented distribution in Western Europe, with isolated breeding nuclei in Spain, France and Italy and a more continuous distribution in Eastern Europe and Asia. Using a combination of nuclear and mitochondrial markers, we assessed the genetic structure and diversity of Lesser Grey Shrike populations from Western Europe, Central Europe and Asia. There was significant genetic differentiation among three major regional groups, one European and two Asian. Genetic diversity measures were lowest in the smallest and most marginal Spanish population. Limited genetic diversity, combined with rapid population decline, suggests the Spanish population may face extinction in the near future.

Keywords: endangered species, genetic structure, inbreeding, peripheral population, subspecies.

Increasingly, conservation biologists are successfully combining population ecology and population genetics in studies focused on the management of endangered and declining species (Frankham *et al.* 2002). Whereas population ecology focuses on processes affecting population demographics, such as habitat deterioration and population growth rates (Sinclair *et al.* 2006), conservation genetics examines geographical structure and temporal changes in genetic variation. Genetic drift and inbreeding are the major phenomena causing loss of genetic variation in small populations (Amos & Harwood 1998). In fragmented habitats, population sizes tend to decline and populations become isolated from each other. This can lead to increased genetic differentiation between populations via the fixation of alleles. Knowledge of the alteration of genetic makeup and/or loss of variation are of interest in conservation biology, because a population is considered to have greater fitness if genetic variation is sufficient to allow for adaptive response to environmental changes, particularly in the face of climate change.

Changes in demography and genetics are often more marked at the edges of a species' range, where numbers are lower and where often fragmented populations may occupy suboptimal habitats (Lesica & Allendorf 1995, Kvist *et al.* 2007). Many species with broad geographical distributions thrive at the centre of the range but decline at the periphery, where they are often considered regionally endangered (Hoffmann & Blows 1994). These peripheral populations are often genetically divergent from the central population and may hold genetic variation that does not exist elsewhere. Thus, their value for future adaptations and evolution can be substantial. Genetic analyses of such

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species include tests for the loss of genetic variation and definition of management units (MUs) and evolutionarily significant units (ESUs; Moritz 1994, Crandall *et al.* 2000) using population genetic, phylogenetic and ecological tools. Genetic data can provide objective measures to pass on to decision-makers.

The Lesser Grey Shrike *Lanius minor* is a socially monogamous long-distance migratory passerine breeding in Eurasia, and has a range extending over 6000 km from east (Kazakhstan) to west (northern Spain) and over 2000 km from south (Turkey) to north (Russia) (Lefranc & Worfolk 1997). Within this range, breeding localities are patchily distributed (especially in Europe) and limited to warm, flat areas with predominantly steppe and/or farmland habitats. The wintering area is centred on the Kalahari basin in southern Africa (Newton 1995, Herremans 1998). All populations migrate between southern Africa and Eurasia through the Middle East and southeastern Europe, with the western and easternmost populations covering about 10 000 km twice a year, making it one of the longest migratory movements among passerines (Lefranc & Worfolk 1997). This shrike is often considered to include two subspecies (Vaurie 1955, Clancey 1980), the smaller and slightly darker *minor* (from Spain to western Russia), and the larger *turanicus* (from the Ural Mountains to central Asia). Some authors consider the species to be monotypic (see Lefranc & Worfolk 1997 for a review) with just slight and clinal morphological variation across the range.

The Lesser Grey Shrike was a fairly abundant bird in central and southern Europe during the 19th century (Lefranc & Worfolk 1997). Thereafter, its population and range sharply declined and contracted, especially in the western half of Europe, where it became extinct in many countries in the 1930s. Because of agricultural intensification, most other European populations underwent moderate decline between 1970 and 2000, with the exception of some central and eastern European countries where the species' demography remains stable (e.g. Hungary; BirdLife International 2004). Currently, the western European populations are restricted to small isolated nuclei in northeastern Spain (fewer than 20 pairs, Giralt & Bota 2003, Giralt & Valera 2007), southeastern France (20–40 pairs, Rufray & Rousseau 2004) and Italy (1000–2500 pairs), whereas the species remains widespread in Eastern Europe (BirdLife International 2004). Data on Asian population trends are scarce, although the species is apparently stable and locally abundant, at least in southern Russia, Georgia (BirdLife International 2004) and Kazakhstan (A. Gavrilov pers. comm.).

The aims of this study were to assess genetic structure among Lesser Grey Shrike populations to identify management units and examine whether the defined races are genetically distinct, to analyse genetic variation within populations to determine whether the decline of the Spanish population has had any genetic effects, and to suggest guidelines for genetic management of the species.

METHODS

Sampling

Studied populations included two breeding nuclei in Spain (Catalonia, 41°34′N, 0°41′E; Aragón, 41°43′N, 0°12′E), two populations from central Europe (Slovakia, 48°36′N, 19°20′E; Hungary, 46°32′N, 20°05′E) and two from Asia (Georgia, 41°45′N, 44°50′E; Kazakhstan, 42°56′N, 70°37′E) (Fig. 1). Spanish birds were sampled during the 2004–2006 breeding seasons, Georgian and Kazakh birds in 2006, Slovakian birds during the 1999 breeding season and Hungarian birds in 1998. Adult birds were caught with clap-nets and mist-nets during nesting. A few nestlings were also sampled in Spain, Slovakia and Hungary. We sampled either blood or feathers.

Laboratory procedures

DNA was extracted from blood samples using the standard phenol-chloroform method and from feather quills using the method described in Kvist *et al.* (2003). Blood stored on FTA cards was prepared for PCR-amplification according to the manufacturer's protocol (Whatman).

Initially, the whole mitochondrial control region was amplified from 10 individuals using primers ND6L (5′-CTAAACAGCCCGAATCGCCC-3′; designed for this study to match a conserved region in the passerine ND6 gene) and laniusftph2 (5′-TCTTGACATCTTCAGTGCCATGC-3′; designed to match the tRNA-Phe gene using available sequences of *Lanius* on GenBank). Based on the obtained sequences, primers NDL6 and STH411 (5′-AAATAACCAGGTTCTCTGGCTTG-3′, originally designed for the Blue Tit *Cyanistes caeruleus*

Figure 1. Current breeding range (dark shaded area) of the Lesser Grey Shrike (del Hoyo *et al.* 2008) and the species' western limit at the beginning of the 20th century (broken line; Lefranc & Worfolk 1997). Sampled populations are marked with small arrows (S, Spain; SL, Slovakia; H, Hungary; G, Georgia; K, Kazakhstan). The long arrow in Saudi Arabia represents the last section of the spring migration route before reaching the breeding areas.

(Kvist *et al.* 2005)) were used to amplify a shorter portion of the mitochondrial control region (including the highly variable first domain and a portion of the central domain). The following PCR profile was used 94 °C for 2 min followed by 35 cycles of 94 °C for 45 s, 50 °C for 45 s and 72 °C for 45 s, with a final extension at 72 °C for 2 min. Sequencing was performed with BigDye$^{\mathrm{TM}}$ v3.0 (Applied Biosystems, Carlsbad, CA, USA) according to the manufacturer's protocol using primer STH411. Sequencing was performed in one direction only and products were run on an ABI 3730 automatic sequencer.

Eight microsatellite loci – *LM1* (T_{m} = 47 °C), *LM2* (T_{m} = 47 °C), *LM3* (T_{m} = 53 °C), *LM4* (T_{m} = 53 °C), *STG4* (T_{m} = 55 °C), *Ppi2* (T_{m} = 50 °C), *Lox1* (T_{m} = 50 °C) and *Pocc6* (T_{m} = 50 °C) – were amplified with the following PCR profile: 94 °C for 2 min followed by 35 cycles of 94 °C for 45 s, 47–55 °C for 45 s and 72 °C for 45 s, and a final extension at 72 °C for 2–10 min. The first five loci were developed from the Loggerhead Shrike *Lanius ludovicianus* (Mundy & Woodruff 1996); *Ppi2* was developed from the Eurasian Magpie *Pica pica* (Martínez *et al.* 1999); *Lox1* is from the Scottish Crossbill *Loxia scotica* (Piertney *et al.* 1998); and *Pocc6* is from the Western Crowned Warbler *Phylloscopus occipitalis* (Bensch *et al.* 1997). The amplified microsatellite alleles were screened on an ABI 3730 automated DNA sequencer and scored using GENEMAPPER v3.7 (Applied Biosystems).

Data analysis

Prior to data analysis, all closely related birds were removed from the dataset. Only one nestling was included per nest and only one parent or nestling was included in the microsatellite data (we did not sample any mother–nestling pairs but fathers were included in the mitochondrial sequence data). Thus, our sample sizes for mitochondrial/microsatellite analyses were: Catalonia *n* = 13/15, Aragón *n* = 4/3, Slovakia *n* = 13/15, Hungary *n* = 9/9, Kazakhstan *n* = 14/16, Georgia *n* = 8/8.

From the mitochondrial data, the nucleotide diversity, theta and haplotype diversity for each population were estimated using DNASP v4.0 (Rozas & Rozas 1999); differences in parameter values among populations were tested with ANOVA. To identify populations that differed from each other, the least-square difference *post hoc* test was applied. DNASP was also used to calculate mismatch distributions, neutrality indices (Tajima's *D* and Fu's *Fs*) and the raggedness index to test for signs of demographic change in the study populations. Smooth unimodal mismatch distributions (tested with raggedness statistics) with significantly negative Tajima's *D* and Fu's *Fs* values are consistent with demographic change, possibly as a consequence of population expansion (Rogers & Harpending 1992). In addition, the software LAMARC v2.1.3 (Kuhner 2006) was used to estimate of the growth rate with a 95% confidence interval based on the coalescent. The default parameters, 10 initial chains (10 000 steps) and two final chains (200 000 steps) were used with the MCMC algorithm, sampling every 20th tree. ARLEQUIN v3.1 (Excoffier *et al.* 1992) was used to estimate pairwise Φ_{ST} values among populations (AMOVA), using Tamura–Nei distances. We also used SAMOVA (Dupanloup *et al.* 2002) to group genetically similar populations and then recalculated Φ_{ST} values based on these groupings. Significance of the pairwise Φ_{ST} values was determined by comparison with a null distribution derived from permuting haplotypes between populations and recalculating Φ_{ST} values 1000 times. The Tamura–Nei substitution model was chosen based on results from MODELGENERATOR v0.83 (Keane *et al.* 2006). Tamura–Nei was the best-fit model based on the Akaike information criteria (AIC) and was the second best model using the Bayesian information criterion (BIC). As it was simpler than the alternative (HKY) and is implemented in most population genetic software, we used the Tamura–Nei model for our analyses. Correlations between genetic and geographical distances were calculated using a Mantel test as implemented in ARLEQUIN (Slatkin's linearized F_{ST} was used for genetic distance and geographical distances were converted into natural logarithms). A parsimony network was constructed with TCS (Clement *et al.* 2000).

The microsatellite data were tested for null alleles, scoring errors and large allele dropout using MICROCHECKER v2.2.3 (Van Oosterhout *et al.* 2004). Hardy–Weinberg (HW) equilibrium was calculated using GENEPOP 4.0 (Raymond & Rousset 1995) and linkage disequilibrium was estimated with FSTAT v2.9.3.2 (Goudet 2001). A Bonferroni correction for multiple tests was applied to *P*-values as implemented in FSTAT. ARLEQUIN was used to calculate observed and expected heterozygosities per locus and population, conduct a Mantel test (as detailed above for mitochondrial data) and sample assignment likelihoods for each of the predefined populations. Assignment likelihoods were computed as log-likelihoods of individual genotypes belonging to a population based on allele frequencies in the population. The inbreeding coefficient F_{IS}, allelic richness and allele distributions were calculated with FSTAT (Goudet 2001) using the rarefaction method to correct for differences in sample sizes. Between-population differences in heterozygosity and allelic richness were tested with ANOVA.

STRUCTURE v2.2 (Pritchard *et al.* 2000) was used to test for clustering of the genotypes into genetically differentiated populations. The number of populations (*k*) was varied from one to six and the assignment probabilities for each individual were estimated using the admixture model with a burn-in of 100 000, 200 000 MCMC replicates and two iterations. In addition, a factorial analysis of correspondence, as implemented in the program GENETIX v4.05 (Belkhir *et al.* 2004), was used to represent genetic variation graphically within and among populations. Pairwise F_{ST} values between populations were calculated with ARLEQUIN and SAMOVA, as explained above for mitochondrial data. Effective population sizes were estimated for the three populations with sample sizes larger than 10 (Spain, Slovakia and Kazakhstan) using the linkage disequilibrium method implemented in NeESTIMATOR v1.3 (Peel *et al.* 2004). BOTTLENECK v1.2.02 (Cornuet & Luikart 1996) was used to test for recent bottlenecks in each population. Bottlenecked populations lose rare alleles faster as heterozygosity decreases, leading to a situation where heterozygosity is higher than expected for a given number of alleles. The distribution of allele frequencies is also affected, shifting towards larger proportions of low-frequency alleles. The program was run with three different mutation models: infinite allele, stepwise mutation and two-phase models (70% stepwise and 30% infinite) with 1000 iterations. To test whether the extent of genetic diversity retained in relation to the number of loci was greater than expected we made use of the Wilcoxon signed-rank test due to our small sample sizes. In addition, the M-ratio (Garza & Williamson 2001) was estimated for each population, again using ARLEQUIN. This index estimates the ratio between the number of alleles and allelic range. A bottleneck reduces the number of alleles faster than the range, and therefore a small ratio indicates a recent bottleneck.

RESULTS

Mitochondrial DNA

The obtained sequences contained no double peaks and no systematic differences could be related to the tissue from which DNA was isolated. Therefore, the possibility of amplifying a nuclear copy of a mitochondrial gene was considered very unlikely.

Table 1. Mitochondrial nucleotide diversity (π), theta (θ), haplotype diversity ($\hat{h}$), number of haplotypes and sample sizes (n) per sampled shrike population.

Population	π	θ	$\hat{h}$	No. of haplotypes	n
Spain	0.00061	0.00154	0.228	3	17
Catalonia	0.00080	0.00168	0.295	3	13
Aragón	0	0	0	1	4
Slovakia	0.00240	0.00168	0.718	3	13
Hungary	0.00289	0.00287	0.750	4	9
Kazakhstan	0.00524	0.00573	0.868	8	14
Georgia	0.00177	0.00201	0.607	3	8

The 385-bp alignment contained 11 segregating sites and 12 haplotypes. The population from Kazakhstan possessed the most mitochondrial variation, with a nucleotide diversity of 0.00524 and eight haplotypes (Table 1). The Spanish population possessed the least variation (subpopulations Aragón and Catalonia combined), with a nucleotide diversity of 0.00061 and three haplotypes. Differences between populations were highly significant for all these parameters (ANOVA for nucleotide diversity: $F = 111.76$, df = 4, $P < 0.01$; for theta: $F = 11.98$, df = 4, $P < 0.01$; for haplotype diversity: $F = 78.27$, df = 4, $P < 0.01$; subpopulations from Spain combined, Table 2). Only one haplotype was found in the small subpopulation from Aragón. The most common haplotype (W1) was shared by 31 individuals and was found in all populations (Table 3, Fig. 2). The second most common type (W2) was shared by eight individuals and was found in Slovakia, Hungary and Spain. Two more haplotypes were found in several populations; haplotype E8 occurred in both the

Table 2. Population pairwise Φ_{ST} values below the diagonal and F_{ST} values above.

Population	Spain	Slovakia	Hungary	Kazakhstan	Georgia
Spain		0.01238	0.01017	0.02592*	0.10154***
Slovakia	0.18849**$_{AC}$		0.01192	0.02437***	0.05599***
Hungary	0.15282**$_{AC}$	0.06004		0.05281**	0.12371***
Kazakhstan	0.17516***$_{ABC}$	0.10981$_{ABC}$	0.09528$_{AB}$		0.03586***
Georgia	0.59890***$_{AC}$	0.45216***	0.25590*$_{A}$	0.15372*$_{ABC}$	

Subscripts below the diagonal represent significant differences in the least-square comparison *post hoc* test following ANOVA ($P < 0.05$).
A, nucleotide diversity; B, theta; C, haplotype diversity.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 3. Distribution of haplotypes among sampled populations. Haplotype designation follows Figure 2.

Haplotype	Catalonia	Aragón	Slovakia	Hungary	Kazakhstan	Georgia	Total
W1	11	4	5	4	5	2	31
W2	1	0	4	3	0	0	8
W3	1	0	0	0	0	0	1
E1	0	0	0	1	1	5	7
E2	0	0	0	0	1	0	1
E3	0	0	0	1	0	0	1
E4	0	0	0	0	0	1	1
E5	0	0	0	0	1	0	1
E6	0	0	0	0	1	0	1
E7	0	0	0	0	1	0	1
E8	0	0	4	0	2	0	6
E9	0	0	0	0	2	0	2
Total	13	4	13	9	14	8	61

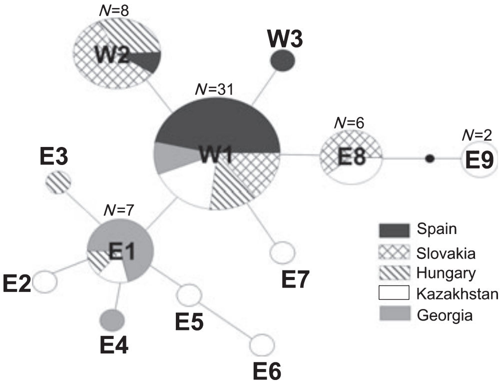

Figure 2. A parsimony network of mtDNA haplotypes. Each circle represents a haplotype with its size proportional to the number of birds sharing that haplotype. The bars connecting the haplotypes represent one nucleotide substitution. The small black circle represents an unsampled or extinct haplotype.

Slovakian and Kazakh populations, whereas E1 was shared among the Hungarian, Kazakh and Georgian populations. The remaining eight haplotypes were rare, as each was found in only one population.

Pairwise Φ_{ST} values (Table 2) were initially estimated between all sample locations. Because pairwise Φ_{ST} values (Table 2) between Catalonia and Aragón were not statistically different, they were combined into one 'Spanish' population. The divergence between the five remaining populations varied from $\Phi_{ST} = 0.060$ (Slovakia and Hungary) to $\Phi_{ST} = 0.599$ (Georgia and Spain). The Spanish population was significantly different from all the other populations, whereas the comparisons involving the Georgian population showed the highest Φ_{ST} values. The overall Φ_{ST} was 0.20 ($P < 0.001$). If populations were grouped according to assumed subspecies (Spain, Hungary, Slovakia representing *L. m. minor*, and Kazakhstan and Georgia representing *L. m. turanicus*), 13.97% of the genetic variation was attributable to between subspecies, 8.89% to between populations within subspecies and 77.15% was within populations, increasing the overall Φ_{ST} to 0.23 ($P < 0.001$). The total Φ_{ST} increased to 0.24 when European populations were grouped together and populations from Georgia and Kazakhstan were considered as separate groups. The highest total Φ_{ST} (0.323, $P < 0.001$) was obtained when the Georgian population was considered separate and all others were grouped into one, the same grouping obtained when using SAMOVA. This, however, increased the among-population within-group variation to 10.75%. A Mantel test suggested a weak trend between geographical and genetic distances ($r = 0.357$, $P = 0.102$).

Tajima's *D* and Fu' *Fs* values were negative for the Spanish population (−1.404 and −2.097), although not significantly so. The mismatch distribution followed the expected distribution of an expanding population and the raggedness index *r* was 0.3496 (ns, 95% CI 0.1289–0.7048). Other populations with a sample size over 10 (Slovakia, Kazakhstan) did not clearly follow either of the expected mismatch distributions, and their Tajima's or Fu's tests were not significant (Fig. 3). However, the combined Lesser Grey Shrike population followed rather closely the expected distribution of a growing population: it had significantly negative Tajima's *D* (−2.614, $P < 0.001$) and Fu's *Fs* (−5.926, $P < 0.02$) values, and a fairly low, but not significant raggedness index ($r = 0.0934$, 95% CI 0.0272–0.4748). LAMARC estimated a high positive growth rate (maximum likelihood estimate for $G = 2732.16$; 95% CI = 2051.96–3418.76), indicating historical expansion of the species' population size. Although we do not know the substitution rate of the Lesser Grey Shrike control region, an estimate of the expansion date of the western populations based on a nucleotide diversity of 0.00189 and the commonly used mitochondrial DNA (mtDNA) substitution rate of 2% sequence divergence per Mya would lead to an expansion date of about 100 000 years ago.

Microsatellites

There was no evidence of null alleles or scoring errors. We found between two and five private alleles per population (Supporting Information Tables S1 & S2). None of the populations showed significant heterozygote deficiency, but significant heterozygote excess was observed in the Georgian population ($P < 0.03$) when estimated across all eight loci. Some individual loci showed significant deviations from HW equilibrium (locus *LS2* in the Spanish and Hungarian populations, locus *Lox1* in the Slovakian population, and *LS3* in the Kazakh population). None of these remained significant after the Bonferroni correction was applied. In general, heterozygosity per locus and population varied from 0 to 1. *LS4* was monomorphic in the

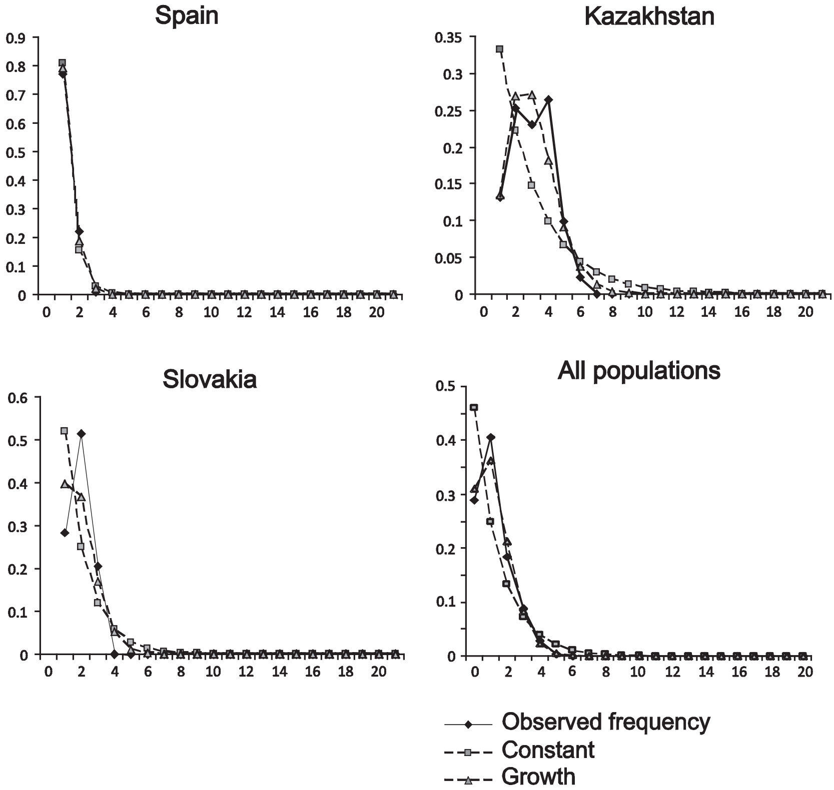

Figure 3. Mismatch distributions with the observed distributions as well as the expected distributions for constant or growing populations are depicted.

Hungarian population and also showed quite low heterozygosity in the other populations (range 0.063–0.375, the Georgian population being the exception, Table 4). Heterozygosity was also low in most populations for loci *STG4* and *Pocc6* (range 0.063–0.750). Linkage disequilibrium was found between *LS2* and *Ppi2* (in the Spanish population, $P < 0.05$) and *LS4* and *STG4* (in Slovakia, $P < 0.01$), but the significance disappeared after Bonferroni correction. Allelic richness (Table 4) was highest in the Hungarian and Slovak populations (4.633 and 4.518, respectively), and the lowest in Spain (3.352), but the difference was not significant (ANOVA: $F = 0.673$, df = 4, $P = 0.615$). In the Spanish population, the mean heterozygosity estimated across loci was also lower (expected heterozygosity 0.489, Table 4) than in the other populations (range 0.531–0.643) but, again, not significantly (ANOVA, observed heterozygosity: $F = 1.057$, df = 4, $P = 0.392$, expected heterozygosity: $F = 0.397$, df = 4, $P = 0.809$, Spanish populations combined), whereas F_{IS} was positive ($P > 0.05$, Table 4). Estimated effective population size was only 3.9 individuals (95% CI 3.2–4.9) in the Spanish population. Other populations, with adequate sample sizes, provided estimates of 35.5 for Slovakia and 28.2 for Kazakhstan (95% CIs were 9.7–118.2 and 16.8–68.11, respectively). The bottleneck test failed to find any evidence of population bottlenecks in any population. This indicates that the present bottleneck has not (yet) reduced the number of alleles relative to heterozygosity in the Spanish population. There was also no shift in the mode of the allele frequency distribution. However, the M-ratio for the Spanish population was only 0.65, suggesting that the number of

Table 4. Expected heterozygosity (H_{exp}), observed heterozygosity (H_{obs}) and allele richness (R) per locus and population. Mean F_{IS} is estimated over all loci for each population. Allelic richness is estimated as the weighted mean for each locus (R).

	Spain			Slovakia			Hungary			Kazakhstan			Georgia			
Locus	H_{exp}	H_{obs}	R	H_{exp}	H_{obs}	R	H_{exp}	H_{obs}	R	H_{exp}	H_{obs}	R	H_{exp}	H_{obs}	R	Mean R
S1	0.772	0.857	4.967	0.710	0.733	5.416	0.810	0.889	6.654	0.841	0.938	6.347	0.833	1	6.000	6.641
LS2	0.644	0.444	3.403	0.811	0.800	6.117	0.784	0.556	6.654	0.802	0.813	5.695	0.767	1	4.000	5.649
LS3	0.401	0.375	2.497	0.513	0.600	3.322	0.314	0.333	3.667	0.688	0.938	3.498	0.725	0.750	5.000	3.641
LS4	0.063	0.063	1.500	0.186	0.200	1.910	0	0	1.000	0.339	0.375	3.387	0.542	0.750	3.000	2.515
STG4	0.191	0.200	2.324	0.503	0.600	4.421	0.307	0.333	2.882	0.460	0.313	3.491	0.542	0.750	3.000	3.574
Ppi2	0.738	0.786	4.394	0.786	0.733	6.185	0.784	0.667	5.667	0.809	0.800	6.126	0.817	0.875	5.000	5.700
Lox1	0.671	0.556	4.749	0.834	0.667	6.859	0.856	1	7.549	0.643	0.688	4.328	0.675	0.500	4.000	5.412
pocc6	0.383	0.389	3.102	0.186	0.200	1.910	0.392	0.444	2.987	0.063	0.063	1.500	0.242	0.250	3.000	2.667
Mean	0.489	0.459	3.352	0.566	0.567	4.518	0.531	0.528	4.633	0.581	0.616	4.282	0.643	0.734	4.125	
F_{IS}	0.051			−0.001			0.007			−0.063			−0.154			

alleles has declined in relation to allelic range. M-ratios for the other populations were 0.71 for Slovakia, 0.87 for Hungary, 0.78 for Kazakhstan and 0.78 for Georgia. According to Garza and Williamson (2001), an M-ratio below 0.68 indicates a reduction in population size when analysed for more than seven loci, i.e. the index suggests a recent bottleneck in the Spanish population.

The program STRUCTURE did not reveal any evidence of genetic structuring between the sampling sites, and the highest log-likelihood obtained was for $k = 1$, i.e. a single panmictic population. Nevertheless, population structure was suggested by the factorial correspondence analysis, in which all the populations cluster separately (Fig. 4). Some structuring was also detected by AMOVA, with overall $F_{ST} = 0.0381$ ($P < 0.001$). It is possible that STRUCTURE failed to detect any differences between the populations due to the small sample size and the number of loci used. The largest pairwise values were found in comparison with the Georgian population (0.056–0.124), whereas the smallest were found between the European populations (0.010–0.012, Table 2). The Spanish population did not differ significantly from other European populations, but the Asian and European populations did, and the two Asian populations differed from each other. Total F_{ST} increased to 0.0508 ($P < 0.001$) when populations were grouped according to subspecies *minor* and *turanicus* and to 0.0525 when three groups, i.e. Europe, Kazakhstan and Georgia, were formed. As with the mitochondrial data, the highest F_{ST} (0.0806, $P < 0.001$) was obtained when all the populations except Georgia were grouped into one, and this grouping arrangement was supported by SAMOVA. This increased the among-group variation to 6.08%, and also the among-population within-group variation to 1.99%. The correlation between gene flow ($F_{ST}/1 - F_{ST}$) and the natural log of geographical distance was calculated using a Mantel test, and was 0.3842 ($P = 0.062$), which is slightly greater than the value obtained with the mitochondrial sequence data. Although the differences between the European populations were small, most of the individuals were correctly assigned to their population of origin (all the Spanish birds, 13 of 15 birds from Slovakia, eight of nine birds from Hungary, 15 of 16 birds from Kazakhstan and all the Georgian birds).

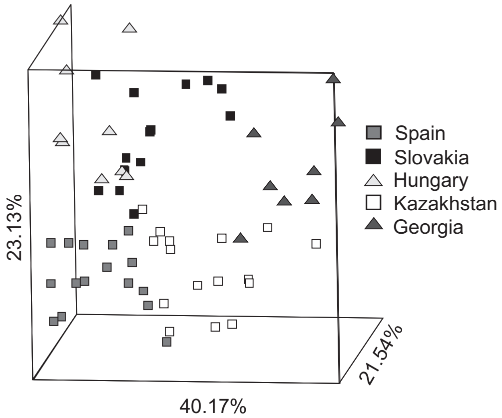

Figure 4. Factorial correspondence analysis with the first three factors presented.

DISCUSSION

Population structure

The endangered Spanish population differed significantly from all others in mitochondrial markers, but only from Caucasian and Asian populations in nuclear markers, even though the distance to the next sampled European breeding population was considerable. This might indicate exchange of breeders among European populations, but a more likely possibility is that the decline and isolation of the Spanish population is still so recent that genetic drift has only had time significantly to affect mtDNA. As mtDNA has a quarter of the effective population size of nuclear markers (assuming equal variance in male and female reproductive success), the former should show the effects of drift four times faster, irrespective of the fact that the mutation rate in microsatellites is generally higher than in mtDNA (see Zink & Barrowclough 2008). Failure to find signs of a genetic bottleneck in microsatellite markers in two of the three bottleneck tests used might also indicate that the observed population declines and resulting isolation are too recent to be detected using genetic data.

AMOVA suggested genetic differentiation between populations within the assumed subspecies *L. m. turanicus*: birds from Georgia and Kazakhstan differed significantly and even more so from each other than from some European populations (Table 2). Therefore, the existence of two subspecies, one from Europe (*L. m. minor*) and one from Asia (*L. m. turanicus*), may need re-evaluation. It is worth highlighting that the Georgian population, which was the most divergent from all others, is surrounded by the Caucasus Mountains, the Black Sea and the Caspian Sea, suggesting stronger physical barriers for this population. On the migration route from Africa to breeding sites, Lesser Grey Shrikes diverge in migration direction from the Arabian Peninsula onwards, heading northwest through Turkey to Europe, north through Georgia to Caucasia and southern Russia, or northeast through Iran to Kazakhstan (Dowsett 1971, Lefranc & Worfolk 1997). This spatial segregation coupled with the high site-fidelity reported at least for adults (Hantge 1957, Kristin *et al.* 2007) could restrict gene flow and therefore explain the relatively greater differentiation between European, Georgian and Kazakh populations. Additional sampling of populations and individuals is necessary to test this conclusion and to reject the alternative possibility that the genetic structure described here has arisen solely through isolation by distance.

Finally, mitochondrial data suggest a historical expansion that may have occurred close to the last glacial period, perhaps beginning during one of the warm interstadial periods. The most common haplotype W1 was found in all populations and lies at the centre of the haplotype network, suggesting that it is an ancestral haplotype already present at the time of the expansion and that most or all other haplotypes evolved subsequently. Similar expansions have been detected for many species whose populations were confined to southern European refugia when glaciers spread across northern latitudes (Newton 2003). Furthermore, current migration routes may retrace ancestral routes of expansion during past colonization (Ruegg & Smith 2002). Thus, it is possible that Lesser Grey Shrikes migrate along flyways that evolved from historical colonization routes after an expansion from a refuge in the Middle East.

Within-population diversity and breeding range fragmentation

Genetic variation is lower in the Spanish population of the Lesser Grey Shrike than in any of the others we sampled. Given that the Spanish population is extremely small, geographically isolated and distant from the continuous breeding range, this is not a surprise. Thus, it seems that the recent reduction in population size coupled with peripheral isolation has resulted in loss of genetic diversity through genetic drift and/or reduced gene flow. Since the beginning of the 20th century, one-third of the previous geographical range of the Lesser Grey Shrike has been lost, almost all in the westernmost parts of its range (Lefranc 1995, 1999, Lefranc & Worfolk 1997). This has resulted in the current distribution of small, isolated and still declining populations in Italy, France and Spain (Lefranc & Worfolk 1997, Rufray & Rousseau 2004, Giralt & Valera 2007).

An alternative explanation for the low genetic diversity of the Spanish population could be a founder effect associated with recent colonization. Wallace and Sage (1969) suggested a recent expansion to northern Spain from France along the

Mediterranean coast in the 1960s. However, the oldest historical record in the Iberian Peninsula is from the 19th century (Vayreda 1883) and additional observations were reported in the 1940s (Heymer 1964). Therefore, it is likely that the species was abundant in France during the 19th century and that the range in Europe contracted mostly during the 20th century. Thus, the low genetic variation of the Spanish population is more probably related to recent fragmentation and population decline than to a recent colonization event. Analysis of historical museum samples (e.g. Goldstein & Desalle 2003, Munõz-Fuentes *et al.* 2005) would enable a more definitive test of these alternatives.

Conservation implications

A census of the Spanish population during 2004 and 2005 recorded 24 and 20 pairs, respectively. In 2006 and 2007, the population size declined to 13 and nine pairs, respectively. The effective population size estimated here is extremely small (3.9), genetic variation is low and F_{IS} is positive (though not significantly), suggesting a substantial loss of genetic diversity in this population. At the same time, the population is facing long-term habitat loss (Giralt & Bota 2003, Giralt *et al.* 2008a). When small, isolated populations face environmental, demographic and/or genetic degradation, the population may end in an extinction vortex: a downward spiral in which the three factors mutually enhance each other, ultimately resulting in extinction (Gilpin & Soulé 1986). The present Spanish population is facing all three threats: habitat loss and instability, population decrease and loss of genetic variability. Moreover, the most likely source of immigrant birds for this population, the nearest French population, is also in serious decline (Rufray & Rousseau 2004), making it likely that the Spanish population will soon become extinct.

Even though the Spanish population (or any of the other studied populations) is not reciprocally monophyletic for mitochondrial markers, as would be required for treating the population as an ESU (*sensu* Moritz 1994), we found significant divergence in mitochondrial haplotype frequencies from all other populations and in microsatellite allele frequencies from the two easternmost populations. This implies that the population should be considered an MU. The eastern populations (Georgia and Kazakhstan) could each form their own MUs, whereas the Slovakian and Hungarian populations could be combined into one. According to Crandall *et al.* (2000), management decisions should be based on ecological and genetic exchangeability between populations at present and in the past. Present genetic exchangeability is clearly rejected in our case and there is support also for rejection of ecological exchangeability between the Georgian, Kazakh and European populations (e.g. due to differences in migration routes). However, there are indications, such as spatial synchronization of western populations (Giralt & Valera 2007), that the Spanish population belongs to the same MU as other European populations (ecological exchangeability). In this case, the present genetic differentiation is simply a result of recent population fragmentation through anthropogenic effects. Thus, our results suggest at least three MUs, given the likelihood of ecological exchangeability between European populations at present and in the past.

Urgently needed conservation measures include large-scale habitat management (Giralt & Valera 2007) to provide breeding sites and allow for gene flow. Habitat management has been tested at a small scale, but its effectiveness has been difficult to estimate reliably (Giralt *et al.* 2008b). Other apparently more effective conservation actions include provisioning of supplementary food and controlling Eurasian Magpies to increase shrike nesting success (Giralt *et al.* 2008b). However, the situation may already be so desperate that even if reproductive output were improved, the population would not recover.

Another possibility could be initiation of a re-introduction or a reinforcement programme to increase genetic variation and population size. Our results imply that if desperate measures are needed to maintain the Spanish population, the stocks used for reinforcement should be drawn from other European populations, preferably the closest ones in France and Italy. It was unfortunate that we were not able to obtain samples from these populations for this study because the genetic variation and structure of these populations should be investigated prior to any reintroduction or reinforcement project. In addition, the origin of founders must be considered in the context of migration behavior, given that directional preferences at least differ among European Lesser Grey Shrike populations (Lefranc & Worfolk 1997).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Microsatellite allele frequencies for each sampled population.

Table S2. Microsatellite allele scores for each individual.

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Table S1. Microsatellite allele frequencies for each sampled population.

Locus/Allele	Spain	Slovakia	Hungary	Kazakhstan	Georgia	All
LS1						
1	0.25	0.033	0	0	0	0.057
2	0	0	0.056	0	0	0.011
3	0.036	0	0.222	0.094	0.063	0.083
4	0.071	0.2	0.056	0.281	0.313	0.184
5	0	0.033	0	0.188	0.188	0.082
6	0.036	0.1	0.111	0.156	0.063	0.093
7	0.286	0.033	0.056	0.031	0.125	0.106
8	0.321	0.5	0.389	0.188	0.25	0.33
9	0	0.1	0.111	0.031	0	0.048
10	0	0	0	0.031	0	0.006
LS2						
1	0	0.067	0.167	0.031	0	0.053
2	0.361	0.367	0.056	0.344	0.375	0.3
3	0.028	0.167	0.111	0.125	0.125	0.111
4	0	0.1	0	0.063	0.25	0.083
5	0.472	0.167	0.444	0.219	0.25	0.31
6	0.139	0	0.111	0.188	0	0.088
7	0	0.1	0.056	0.031	0	0.037
8	0	0	0.056	0	0	0.011
9	0	0.033	0	0	0	0.007
LS3						
1	0	0	0	0	0.063	0.013
2	0	0.033	0.056	0.031	0.188	0.062
3	0	0.067	0.056	0.25	0.125	0.099
4	0.75	0.667	0.833	0.438	0.125	0.563
5	0.219	0.233	0.056	0.281	0.5	0.258
6	0.031	0	0	0	0	0.006
LS4						
1	0	0.1	0	0.031	0.313	0.089
2	0	0	0	0.094	0	0.019
3	0.969	0.9	1	0.813	0.625	0.861
4	0	0	0	0.031	0.063	0.019
5	0.031	0	0	0.031	0	0.013
STG4						
1	0.033	0.033	0	0.031	0	0.02
2	0	0.1	0	0.031	0.313	0.089
3	0	0.033	0.056	0.188	0.063	0.068
4	0.9	0.7	0.833	0.719	0.625	0.755
5	0.067	0.1	0.111	0.031	0	0.062
6	0	0.033	0	0	0	0.007
Ppi2						
1	0	0	0.056	0	0	0.011
2	0	0.033	0	0	0	0.007

Locus/Allele	Spain	Slovakia	Hungary	Kazakhstan	Georgia	All
3	0.036	0.033	0.056	0	0	0.025
4	0.286	0.367	0.333	0.133	0.188	0.261
5	0.214	0.167	0.333	0.267	0.188	0.234
6	0	0.033	0	0.067	0.313	0.083
7	0	0.033	0.056	0.067	0.063	0.044
8	0.393	0.267	0.167	0.333	0.25	0.282
9	0	0.033	0	0.067	0	0.02
10	0.071	0	0	0.067	0	0.028
11	0	0.033	0	0	0	0.007
Lox1						
1	0	0	0.056	0	0	0.011
2	0	0.067	0.056	0	0	0.024
3	0	0.033	0.056	0	0	0.018
4	0.194	0.167	0.167	0.188	0.5	0.243
5	0.528	0.333	0.333	0.563	0.313	0.414
6	0.167	0.133	0.167	0.094	0.063	0.125
7	0.028	0.167	0.111	0.031	0.125	0.092
8	0.028	0.033	0.056	0.125	0	0.048
9	0.028	0	0	0	0	0.006
10	0.028	0.033	0	0	0	0.012
11	0	0.033	0	0	0	0.007
pocc6						
1	0	0	0	0	0.063	0.013
2	0	0	0	0.031	0.063	0.019
3	0	0	0.111	0	0	0.022
4	0.778	0.9	0.778	0.969	0.875	0.86
5	0.139	0.1	0.111	0	0	0.07
6	0.056	0	0	0	0	0.011
7	0.028	0	0	0	0	0.006

Table S2. Microsatellite allele scores for each individual

Population Individual	Locus LS1		LS2		LS3		LS4		STG4		Ppi2		Lox1		pocc6	
Spain																
LM1	211	213	180	192	114	114	190	190	138	138	236	244	271	271	178	180
LM2	179	201	180	192	114	114	190	190	130	138	236	244	271	271	178	180
LM3	211	213	180	180	114	114	190	190	138	140	238	254	269	271	178	180
LM4	179	205	180	190	114	116	190	190	138	138	238	244	269	273	178	178
LM6	211	213	190	190	114	116	190	190	138	138	236	244	269	269	178	178
LM7	179	211	190	190	114	114	190	190	138	138	236	244	273	273	178	178
LM9	211	211	180	190	116	116	190	190	138	138	238	244	269	271	178	178
LM10	179	213	192	192	114	114	190	190	138	138	236	244	271	271	178	180
LM11			180	180									271	271	178	178
LM12			180	190	114	114	190	190	138	138			271	271	178	178
LM13			190	190									271	279	178	182
LM14			190	190	114	118	190	194					277	283	182	186
LM15	213	213	190	190	114	114	190	190	138	138	236	254	271	273	178	178
LM66	211	213	180	180	114	116	190	190	138	140	244	244	269	271	178	178
LM67	205	211	180	190	114	116	190	190	138	138	238	244	271	271	178	178
LM16	179	213	180	190	114	114	190	190	138	138	234	244	269	273	178	178
LM18	179	213	190	192	114	114	190	190	138	138	238	246	271	271	178	178
LM19	179	213	182	192	114	114	190	190	138	138	236	236	271	273	178	180
Slovakia																
LM20	205	209	186	190	114	116	190	190	132	138	238	246	283	285	178	178
LM21	213	213	180	180	114	114	190	190	138	138	236	244	269	275	178	178
LM22	205	213	182	186	114	114	190	190	138	138	236	244	269	275	178	180
LM23	213	215	180	180	114	116	180	190	132	138	236	238	269	275	178	180
LM24	213	213	178	180	110	112	180	190	136	138	244	256	271	277	178	178
LM25	205	211	178	182	114	116	180	190	138	142	240	244	273	275	178	178
LM26	213	213	186	190	114	116	190	190	138	140	244	244	267	275	178	178
LM27	209	213	182	198	114	116	190	190	132	138	236	244	271	271	178	180
LM28	207	215	180	190	114	114	190	190	138	138	236	238	271	271	178	178
LM29	209	213	180	194	114	116	190	190	138	138	236	236	271	273	178	178
LM30	213	215	180	182	114	114	190	190	138	138	234	242	265	273	178	178
LM31	205	213	190	190	114	114	190	190	138	140	236	236	271	271	178	178
LM32	179	205	180	182	112	114	190	190	138	140	238	238	265	273	178	178
LM33	205	213	180	194	114	116	190	190	130	138	232	236	271	271	178	178
LM34	213	213	180	194	114	114	190	190	138	138	236	244	269	269	178	178
Hungary																
LM35	211	215	190	196	114	114	190	190	138	138	236	238	271	273	178	178
LM36	201	213	178	190	114	114	190	190	138	140	230	238	269	273	178	178
LM37	201	213	178	190	114	114	190	190	138	138	242	244	271	277	178	178
LM39	213	213	180	194	114	114	190	190	138	138	236	238	271	275	178	178
LM40	209	213	190	190	114	114	190	190	138	138	236	236	269	273	178	178
LM41	205	213	178	190	112	114	190	190	138	138	234	236	261	267	178	180
LM43	201	209	192	192	114	116	190	190	136	138	238	238	265	271	176	178
LM45	201	215	182	182	110	114	190	190	138	140	236	238	269	271	176	178
LM48	199	213	190	190	114	114	190	190	138	138	244	244	271	275	178	180
Kazakhstan																
LM50	205	207	180	190	112	114	190	190	136	138	242	244	271	273	178	178
LM51	205	207	180	180	114	116	190	190	136	136	244	244	271	271	178	178
LM52	209	213	180	180	114	116	190	190	138	138	244	244	269	269	178	178

	Locus															
Population	LS1		LS2		LS3		LS4		STG4		Ppi2		Lox1		pocc6	
Individual																
LM53	205	215	180	186	114	116	190	190	136	136	238	238	271	277	170	178
LM54	201	209	180	190	114	116	190	190	138	138	238	244	269	271	178	178
LM55	205	209	190	192	112	114	190	190	138	138	238	254	271	277	178	178
LM56	205	209	180	190	112	112	190	190	138	138	238	244	271	271	178	178
LM57	213	217	192	192	112	114	180	190	138	138	240	246	271	275	178	178
LM58	201	209	180	182	112	114	190	190	138	138	236	244	271	271	178	178
LM59	201	211	182	192	114	116	182	190	138	138	236	244	269	271	178	178
LM60	205	207	182	192	114	116	182	190	138	138			271	273	178	178
LM61	205	207	178	180	110	112	182	190	136	138	238	240	269	271	178	178
LM62	213	213	186	190	114	116	190	190	138	140	238	254	269	273	178	178
LM63	205	207	190	194	114	116	190	192	130	138	236	238	271	277	178	178
LM64	205	213	182	192	114	116	190	190	138	138	242	244	271	271	178	178
LM65	207	213	180	190	112	114	190	194	132	138	236	246	271	277	178	178
Georgia																
LM68	207	211	180	186	114	116	190	190	138	138	236	238	269	269	170	178
LM69	205	207	180	186	114	116	190	190	138	138	240	240	269	269	178	178
LM70	205	213	180	190	112	116	180	190	132	138	240	244	271	271	178	178
LM71	211	213	182	190	112	116	180	190	132	138	240	244	269	271	178	178
LM72	207	213	182	190	108	116	180	190	132	138	238	244	271	273	168	178
LM73	205	213	180	190	110	116	180	190	132	138	238	244	271	275	178	178
LM74	205	209	180	186	116	116	190	192	132	138	236	242	269	269	178	178
LM75	201	205	180	186	110	110	180	190	136	138	236	240	269	275	178	178

CAPÍTOL 5

Return rates vs. reproductive rates and the viability of a small and marginal population of Lesser Grey Shrike

Taxes de retorn vs. taxes reproductives i viabilitat d'una població petita i marginal de trenca

Giralt, D., Mañosa, S, Brotons, LL. & Valera, F. (en preparació). Return rates versus reproductive rates and the viability of a small and marginal population of Lesser Grey Shrike. Manuscrit.

Taxes de retorn vs. taxes reproductives i viabilitat d'una població petita i marginal de trenca

David Giralt, Santiago Mañosa, Lluís Brotons i Francisco Valera

RESUM: L'anàlisi de viabilitat poblacional (PVA) s'ha convertit en una eina freqüentment utilitzada per avaluar el risc d'extinció de les poblacions o espècies, així com per identificar els paràmetres clau per a la viabilitat poblacional. Aquestes anàlisis permeten planificar amb major eficàcia les possibles accions de gestió dirigides a determinats paràmetres demogràfics. En aquest estudi, l'objectiu ha estat explorar el paper dels paràmetres reproductors i de les taxes de retorn (que inclouen la supervivència i la filopàtria) en el declivi i el risc d'extinció d'una població petita, perifèrica i amenaçada de Trenca (*Lanius minor*). Vam elaborar un primer model amb la mida de la població de l'any 2006 (25 exemplars) i les principals taxes vitals estimades a partir dels anys d'estudi previs (2002-2005), el qual preveu una taxa de creixement negativa i una probabilitat d'extinció de 0,98 a 10 anys vista. La comparació de diferents escenaris demogràfics posa de manifest que tant la supervivència dels adults com la dels ocells de primer any, té un major efecte sobre la dinàmica de la població que l'èxit reproductor i la taxa d'envol. A més a més, les prediccions mostren que fins i tot millorant les taxes de reproducció fins a nivells molt alts, a través de fortes mesures de gestió contínues en el temps, la població continuaria en declivi, fet que demostra que la taxa de retorn és massa baixa per a assegurar la persistència de la població. Les dades posteriors a 2006 han recolzat les prediccions del model, ja que la població va seguir disminuint malgrat la millora de l'èxit reproductor. Una vegada identificada la taxa de retorn com la causa principal de la disminució, també discutim el paper de la immigració i la estocasticitat en la dinàmica de les poblacions petites i marginals. El nostre estudi posa en relleu la necessitat de monitoritzar les poblacions abans que arribin a xifres massa baixes i per tal d'entendre adequadament la seva dinàmica i planificar millor l'estratègia de gestió.

Return rates versus reproductive rates and the viability of a small and marginal population of Lesser Grey Shrike

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Keywords: population viability analysis, conservation planning, survival, extinction, isolation, Lanius

Compliance with Ethical Standards

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

Research involving animals: We had the permit (each year) for capturing and marking birds (specific for shrikes) from the Government in Catalonia (Departament d'Agricultura, Ramaderia i Medi Ambient de la Generalitat de Catalunya) (http://web.gencat.cat/ca/tramits/tramits-temes/Autoritzacio-per-a-la-captura-cientifica-danimals?category=75c244ce-a82c-11e3-a972-000c29052e2c). Our work was previous to the Directive 2010/63/EU of the European Parliament and of the Council of 22 September 2010 on the protection of animals used for scientific purposes.

Abstract

Population Viability Analysis (PVA) has become a common tool used to assess the extinction risk of populations or species as well as to identify the key parameters for population viability. These analyses allow planning management actions on targeted demographic parameters more effectively. In this study, we aimed to explore the proximate role of reproductive

parameters and return rate (encompassing survival and philopatry) on the decline and the extinction risk of a threatened, small and peripheral bird population of Lesser Grey Shrike (*Lanius minor*). We ran a first model with the 2006 population size (25 birds) and the main vital rates estimated during the previous years (2002-2005) that predicted a negative growth rate and an extinction probability of 0.98 in 10 years. The comparison of different scenarios revealed that both adult and first-year survival had a greatest effect on population dynamics than both fledgling and breeding success. Furthermore, predictions showed that even improving reproductive rates to very high levels, by continuous and strong management actions, the population still decreased, showing that return rate was too low to ensure population persistence. Post-2006 data supported model predictions, when the population continued to decline in spite of an improvement of breeding success. Once identified return rate as the main cause of the decline, we also discuss the role of immigration and stochasticity on the dynamics of small and marginal populations. Our study highlights the need of monitoring populations before they reach low numbers to properly understand their dynamics and to better plan management strategy.

Introduction

Estimating the risk of extinction of threatened species is a crucial aspect of population ecology and conservation biology (Purvis et al. 2000; Reed et al. 2003). Moreover, making quantitative predictions on population viability using simulation tools that allow incorporating environmental and demographic stochasticity into models, can substantially improve our understanding about which demographic rates are more significant on population dynamics and fate (Lacy 2000; Morris & Doak 2002). For these reasons, Population Viability Analyses (PVA) has become a common tool used to compare and prioritise between alternative management options (Purvis et al. 2000; Morris & Doak 2002; Naujokaitis-Lewis et al. 2008).

Several factors and life history traits are behind the different susceptibility among species to get extinct, such as having a small geographical range, a narrow niche breath, a high trophic position or a delayed maturity (McKinney 1997; Purvis et al. 2000). Within farmland passerines, a higher vulnerability to decline is associated with specialists, low parental investment strategies, long-distance migrators or species with relative small brain size (Shultz et al. 2005; Pocock 2011). At the population level, isolation and small population sizes increase the extinction probability as a consequence of the combined effects of demographic and genetic factors (stochasticity and inbreeding) in the so-called small-population paradigm (Simberlof 1986; Caughley 1994). In addition, the peripheral distribution areas have been often associated with a higher risk of extinction than central ones due to smaller and higher variable population sizes in the periphery (Hengeveld 1990; Curnutt et al. 1996). A lower fit of marginal than central populations to their respective environment would finally result in a higher risk of decrease and extinction in the edge (Gaston 1994; Curnutt et al. 1996).

Population size and dynamics are mainly affected by four processes: natality, immigration, mortality and emigration (Hanski 1999). In small populations with long-term population decreases or range contractions, stochasticity and inbreeding can also play a relevant role on their fate, as well as density-dependent processes (Caughley 1994; Morris & Doak 2002; Grotan et al. 2009). Therefore it is crucial to understand the relative contribution of those demographic parameters on population dynamics of threatened population or species, if any conservation action has to be applied efficiently (Morris & Doak 2002; Naujokaitis-Lewis et al. 2008).

The Lesser Grey Shrike is a well-suited study species for extracting useful lessons from a conservation point of view. It is an endangered bird passerine throughout Europe, having declined markedly in abundance and range in the last decades in the continent, although it is still widespread in Asia (Lefranc 1993; Kristin 2008). The main suggested causes for such decline are general processes like loss of habitat (agricultural intensification) and adverse weather on their breeding grounds (Lefranc 1993; Lefranc & Worfolk 1997; Isenmann and Debout 2000). Herremans (1998) also noted the possible role of pesticide use and drought on the non-breeding grounds, in southern Africa. This species shows some of the above-mentioned features associated with an increased extinction risk, namely: i) it is a farmland specialist (Lefranc 1993; Kristin 2008); ii) it has narrow niche breath in terms of prey type and size (Kristin 2008); iii) it performs one of the largest migration among passerines within the West Palearctic (Lefranc & Worfolk 1997; Kristin 2008); iv) in our study area at the south westernmost range of the species there still remains a relict, peripheral population whose decline has been studied with some detail (Giralt &Valera 2007; Giralt et al. 2008; Giralt et al. 2010; Kvist et al. 2011).

In this study, we aimed to investigate the roles of reproductive parameters and return rates (mortality and emigration) on the extinction risk of a small and peripheral Lesser Grey Shrike (*Lanius minor*) population in Catalonia (NE Spain). For this, we: i) parameterised a population viability model on the basis of population data for the period 2002-2005 and projected such model into the future; ii) explored the relative role of survival and reproduction success on growth rate; iii) used post-2006 data and management conservation measures applied to the species in the area to assess the predictions of the PVA model and the potential of these measures to reverse species population trends.

Methods

Study species

The Lesser Grey Shrike is a long-distance migrant passerine that overwinters in the Kalahari basin, southern Africa, and breeds in warm flat, open areas in Eurasia, extending from Kazakhstan in the east to northern Spain in the west (Lefranc & Worfolk 1997). At the start of this century, the species had almost disappeared from west Europe, except from Italy (1000-2500 pairs) (BirdLife International 2004), southeast France (15-36 pairs, A.Pichard, com. pers.) and northeast Spain (20-24 pairs) (Giralt & Valera 2007; Giralt et al. 2010). The breeding period typically extends from mid May to mid July. Incubation lasts 15-16 days and the nestling period normally between 16-18 days. It is a monogamous and relatively gregarious species, breeding territories usually covering 6-8 hectares (Lefranc & Worfolk 1997). In Europe it is restricted to farmed areas mainly composed by herbaceous crops, fallows and meadows, sometimes with open scrub vegetation (Lefranc & Norfolk 1997; Giralt et al. 2008). Diet mainly consists of insects, particularly coleopterans and orthopterans, though sporadically can include vertebrates (Kristin 1995).

Study area and population

The Spanish Lesser Grey Shrike population is located in the Ebro basin, NE Spain, a flat area with a Mediterranean continental and dry climate (300-400 mm of annual rainfall). Two small nuclei are known, one located in Catalonia and a smaller one, located 40 km away, in Aragon (Giralt et al. 2010). The present study focuses on the Catalonian population, which represented 82% of the Spanish breeding population on 2002, holding 19 breeding pairs (and only 1 pair in 2010). The size of the study area is of 35-40 km^2 and comprised the strict breeding grounds, where all the pairs have been recorded between 2002 and 2010, and a buffer area of 5 km wide. The Spanish population represents the westernmost breeding locality within the whole breeding distribution and the end of the western migratory route (Kristin 2008; Giralt et al. 2010). The nearest population is located 300 km northeast, in the Mediterranean coast of France (Bara 1995; Isenmann & Debout 2000).

Since 2006 and with the objective to quickly reverse the trends of this declining population, two main management actions have been applied: 1) daily food supplementation of every breeding pair from the start of incubation until fledglings were approximately 25 days old (10 days after leaving the nest) and 2) daily local control of magpies (*Pica pica*) in the breeding area from April until July using Larsen-like traps (Bub 1991). Food supplementation targeted the improvement in fledgling success by reducing chick mortality in the nest (estimated at 19% of the hatched eggs, unpublished data), while magpie control aimed at increasing the percentage of breeding pairs that successfully fledged at least 1 fledgling. Available evidence (based on direct observation of predation events) and high Magpie densities in the study (almost 40 adults/km^2) indicated that the species played a potential role as nest predators in the area (Estrada et al. 2004; unpublished data). Food supplementation was carried out by the same researchers that monitored the population, while magpie control was carried out by the national ranger brigade.

Data collection

After the first population size estimation performed on 1998, a closer annual monitoring of each breeding pair started in 2002 (19 pairs). It included an intense field prospection to locate all breeding pairs and nests (May-June) as well as the subsequent monitoring of each nest until the fledglings left the breeding territory (July-August). Breeding pairs were located by two persons prospecting the study area eight hours per day, searching for birds and possible reproduction behaviours such as nuptial flights, nest material collection and intraspecific interactions. Peripheral areas with lower habitat availability (i.e. absence of big trees for nesting) around the known breeding area were also regularly visited during the entire breeding period (May-July). The strong field effort applied allowed us to assume that most or even all pairs and unpaired birds were found and, if ringed (see below), identified each year.

Breeding performance of each pair was monitored from incubation onwards on the basis of daily observations with binoculars and telescope and supported by 1-3 visits to each nest between the start of incubation until the fledglings left the nest. Annual breeding failure was calculated as the percentage of nesting pairs in the population that failed to produce any fledgling (Table 1). Nests were closely observed with telescope around the calculated date of fledgling and during 1-2 subsequent days so as to count the fledglings and to avoid underestimating fledgling success due to possible early mortality events after leaving the nest. Annual fledgling success was calculated as the mean number of fledglings (leaving the nest) per successful pair (Table 1). Both breeding and fledgling success were annually estimated with data from most pairs of the population, with a mean percentage of annually monitored pairs of 99±3% and 97±4% respectively, across 4 years of study (2002-2005).

Since 2004, a random sample of adult and young birds were ringed and individually marked with combinations of one or two metal colour rings. Adult birds were cached with clap nets or mist nets at their breeding territories while young birds were marked during the last visit to the nest or, in some case, with the help of mist nests after they had fledged. Each year all birds were closely observed to identify them on the basis of their colour ring combination. Adult male and first-year return rates were annually estimated as the percentage of returned ringed birds in relation to the number of ringed birds (old and newly marked) identified the previous year. We therefore use the term return rate or, inversely, apparent mortality, to refer to the combination of true survival plus natal/breeding philopatry. For the baseline PVA model (see below) we calculated the mean return rate across the first 2 years with data (2004/05 and 2005/06). During these 2 years, 15 out of 36 available adult males (42%) and 27 out of the 71 juveniles that fledged (38%) were marked, ensuring a good representation of the population behaviour, despite the relative low sample sizes. Due to low sample size, adult female return rate and was assumed to be equal to male return rate in all simulations. Given that breeding philopatry is considered to be higher for males than for females in this species (Lefranc 1993; Kristin et al. 2007), our assumption of equal return rate between sexes will give slightly optimistic results, but does not alter the relative role of the parameters on the viability of the species, thus allowing us to compare model predictions.

Table 1: Input parameters in the baseline scenario for the PVA of the Lesser Grey Shrike (*Lanius minor*) in Catalonia (NE Spain)

Parameter	***Value***	**Source**
Initial population size (N)	25	own data
Extinction definition	no animals of one or both sexes	-
Inbreeding depression	3.14 lethal equivalents 50% due to lethal alleles	Miller & Lacy 2005; Ralls et al. 1988
Reproductive system	monogamy	Valera et al. 2003
Density dependent reproduction or mortality	No	Kristin et al. 2000
First age of reproduction	1	Lefranc 1993
Maximum breeding age (senescence)	10 years	assumed
Sex ratio at birth	1:1	A.Llopis com.pers
% of adult males in the breeding pool	100% (monogamy)	Lefranc 1993;
% adult females successfully breeding (SD)	68.9 (6.8) (n=4 years)	own data (2002-2005)
Fledgling success: mean progeny per successful breeding female (SD)	3.8 (0.2) (n=4 years)	own data (2002-2005)
% First year mortality (SD)	80.6 (9.8) (n=2 years)	own data (2004-2005)
% Adult mortality (1<=age<=10) (SD)	55.0 (7.1) (n=2 years)	own data (2004-2005)

PVA modelling

PVA to asses the extinction probability and the deterministic and stochastic growth rate were conducted using the software VORTEX (version 9.99b), an individual-based simulation program that can model the effect of deterministic and stochastic processes on the dynamics of populations (Lacy et al. 2009). A baseline model and thirteen alternative scenarios were built, each one with one thousand iterations (Miller and Lacy 2005), with an initial population equal to the estimated size in 2006 (25 birds) and for a time frame of 10 years (Table 1). It is worth to note that the data of the main demographic parameters (breeding success, fledgling success and return rates) needed for model predictions were obtained on the basis of an intense field work and not from bibliography (Table 1). We first built a baseline model using the vital rates observed in the period 2002-2005 to know the expected population dynamics, thus simulating no changes on population conditions after 2005. Thirteen alternative scenarios were built to explore the effects of possible management actions on the persistence of the species and to identify which vital rates had a greater impact on population growth rate and extinction probability. In each alternative scenario, we improved the value of only one parameter by a 10%, 20% or 30% increase, keeping the rest of parameters unchanged. Four different parameters were changed in this way: fledgling success, breeding success and adult and first-year return rate. Finally, to explore if population was still viable in the case of applying a strong management effort, we run a final model where both breeding and fledgling success improved by 20% in relation to baseline scenario, without any change on return rates. As a result, fourteen scenarios were built (1 baseline and 13 alternative scenarios).

For all models we assumed the population to have a stable age distribution at the start of the simulation, which is calculated by Vortex software (Miller & Lacy 2005). Extinction was defined to occur when in a given year one of the sexes was absent. Inbreeding depression was included in all models using the same values suggested by Lacy et al. (2005) (Table 1), because some degree of genetic loss already at that time has been demonstrated for the whole Spanish population (Kvist et al. 2011). We assumed a null immigration, because the loss of genetic diversity in the Spanish population is assumed to be a consequence of isolation and long-term decline (Kvist et al. 2011), and because the stronghold of the species (Eastern Europe) is 1500 km far from the study population. In fact, only one bird out of more than 140 birds ringed in both Spanish populations during almost 10 years, moved between populations (unpublished data). This negligible flow between close populations (40 km between both Spanish nuclei) strongly suggested that immigration from more distant locations is likely to be irrelevant.

Results

Effect of reproductive and return rates on population dynamics

Under the baseline scenario the predicted population trend was clearly negative (Figure 1) both from deterministic (r=-0.35) and stochastic growth rate (r=-0.39±0.39) (Table 2). A high probability of extinction 5 and 10 years later was predicted: 0.53 and 0.98, respectively (Figure 2).

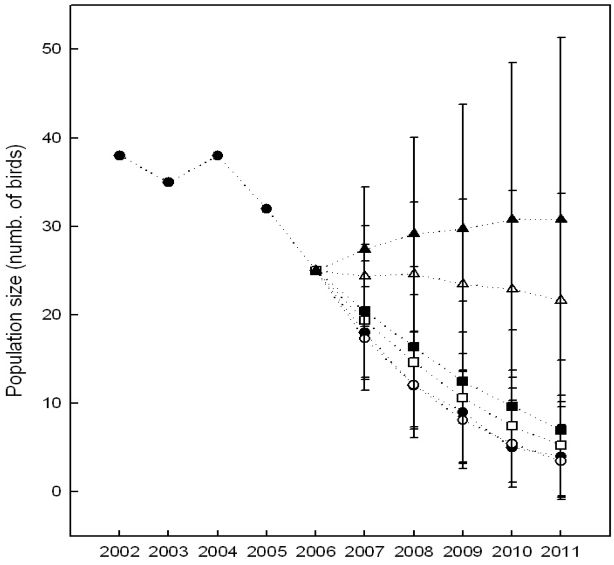

Figure 1 Actual evolution of the Lesser Grey Shrike population size during the study period (black circles) and predicted population size (mean and standard deviation) under some of the scenarios: Baseline model (BM) (white circles); BM with a 30% increase of breeding success (white squares); BM with a 30% increase of fledgling success (black squares); BM with a 30% decrease of adult mortality (white triangles); BM with a 30% decrease of first-year mortality (black triangles).

Both adult and first-year return rate, had a greater impact than breeding parameters on population growth rate and thus on extinction risk and population viability (Figure 2 and Table 2). For example, following an increase of 20% in the return rate, the extinction risk after 10 years was predicted to substantially decrease from 0.98 to 0.44, while the same improvement on the breeding success only reduced the extinction probability from 0.98 to 0.95. Actually, the improvement of any of the two main reproductive rates had a negligible effect on the viability of the population (Figure 2 and Table 2). Even after the improvement of both reproductive rates together, a negative growth rate persisted: when breeding success and fledgling success were set at almost 90% and 5.0 fledglings/pair, respectively, deterministic and stochastic growth rate continued to be negative (r_{det}= -0.13 and r_{stoch}= -0.26±0.40) and the extinction probability at 10 years remained very high (0.79) (Table 2). On the contrary, the extinction at 10 years was already very unlikely when either adult (PE=0.12) or first-year (PE=0.17) return rate increased by 30%, with the stochastic growth rate approaching zero, which means almost population stability (Figure 2).

Table 2: Predicted values of extinction probability (PE) after 10 years and deterministic and stochastic growth rate under the different simulated scenarios assessed in the PVA of the Lesser Grey Shrike (*Lanius minor*) in Spain. Mortality is introduced in the simulations calculating the inverse of the return rate.

Scenario	*PE 10 years*	*Det r*	**Stoch r**
Baseline scenario (BM)	0.98	-0.35	-0.39±0.39
Fledgling success +10%	0.96	-0.30	-0.36±0.38
Fledgling success +20%	0.92	-0.24	-0.31±0.40
Fledgling success +30%	0.88	-0.19	-0.30±0.40
Breeding success + 10%	0.96	-0.30	-0.36±0.39
Breeding success + 20%	0.93	-0.25	-0.34±0.39
Breeding success + 30%	0.93	-0.21	-0.33±0.39
Adult return rate + 10%	0.84	-0.23	-0.28±0.35
Adult return rate + 20%	0.47	-0.11	-0.18±0.29
Adult return rate + 30%	0.12	-0.01	-0.07±0.25
First-year return rate + 10%	0.83	-0.18	-0.27±0.35
First-year return rate + 20%	0.45	-0.03	-0.15±0.34
First-year return rate + 30%	0.17	+0.09	-0.03±0.30
Breeding success +20% and Fledgling success +20%	0.79	-0.13	-0.26±0.40

Situation after 2006: improvement of breeding success but collapse of the population

After 2006 and coinciding with the start of a strong management action, breeding success clearly improved to levels around 90%, while fledgling success remained very similar to previous years and return rates slightly decreased (Table 3). This new situation would roughly match one of the simulated scenarios (+20% increase in breeding success), that predicted a negative deterministic and stochastic growth rate of -0.25 and -0.34±0.39, respectively (Table 2). In agreement with model prediction, this 20% increase on breeding success solely was not enough to stop the decline and avoid quasi-extinction (Figure 2), as the loss of breeding pairs continued from 2006 onwards, and in 2010 and 2011 only 1 pair bred.

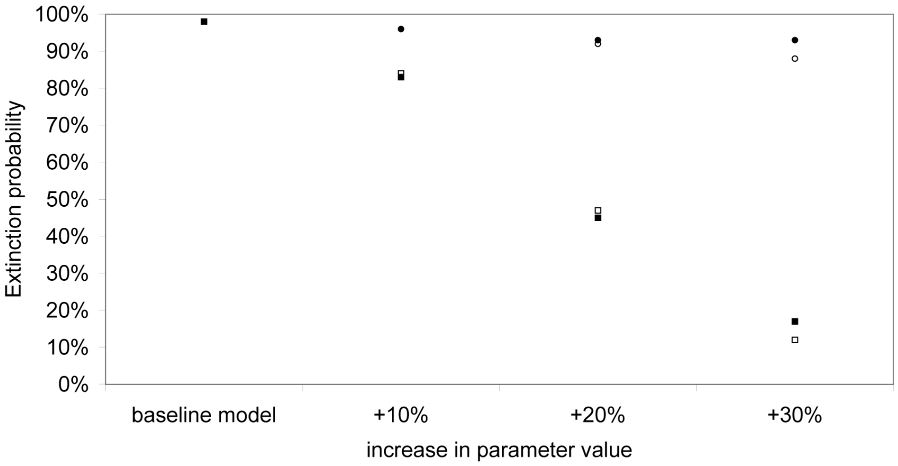

Figure 2 Extinction risk after 10 years is plotted as a function of the relative increase of each of the four demographic parameters analysed: fledging success (white circles): breeding success (black circles); adult return rate (white squares); first-year return rate (black squares).

Table 3: Comparison of demographic parameters before and after management action took place. [a] number of nests refers to the breeding parameters while number of ringed birds refers to return rates

Reproductive rates	**Before (2002-2005)**			**After (2006-2008)**		
	Mean ±SD	N (years)	Numb. of nests /marked birds[a]	Mean ±SD	N (years)	Numb. of nests /marked birds[a]
Fledgling success	3.8±0.2	4	67	3.9±0.9	3	23
Breeding success	69±7%	4	68	90±10%	3	23
Return rates	**Before (2004-2005)**			**After (2006-2007)**		
Ad. (male) return rate	45±7%	2	15	38±26%	2	12
First-year return rate	19±10%	2	27	13±8%	2	31

The strongest decline of the population occurred between 2007 and 2008 breeding seasons, when adult return rate dropped to 11% (1 marked male out of 5 males and 4 females returned on 2008). Surprisingly, apparent mortality seemed to hit particularly males, because sex-ratio became strongly biased toward females up until 2010: 1 male per every 3 females was the average sex-ratio (range 1:2- 1:4) across those years (2008-2010). Before 2008 only few solitary males had been observed, sex ratio being quite balanced, with an average of 1:0.9 (range 1:0.8 - 1:1) (3 years with data: 2005-2007).

Discussion

In this study, for the first time an attempt has been made to identify the proximate causes of the decline and extinction risk of a Lesser Grey Shrike population, performing a population viability analysis, where the role of the main vital rates are together evaluated. Our analysis showed that assuming no immigration, the main Spanish population during the last decade has been suffering at least from low return rates, making the extinction unavoidable in the near future without any significant change in that vital rate. First, we predicted a high extinction risk (0.98) at short term (year 2016) as a consequence of the negative growth rates and the already low starting population size. Furthermore, analysis revealed that growth rate was much more sensitive to changes in return rate than on reproductive rates. Actually, only an increase of 30% on adult or first-year return rate reduced the extinction risk to low levels (i.e. less than 20%) at 10 years. Our results also indicate that an improvement of reproductive rates through management options would have an almost null effect on future growth rate and population dynamics.

Observational data corroborated at some point the model predictions because the population decline continued after 2006, even though breeding success had improved to a rate of 90%. Therefore, both observational and modelization data give support to a major role of return rates both of adults and first-year birds, on population dynamics. The long-term decline of the Lesser Grey Shrike in Europe has traditionally been linked to habitat loss and food shortage due to agriculture intensification, adverse weather or pesticides (Lefranc 1993; Lefranc & Norfolk 1997; Herremans 1998). More locally, an effort has been made to understand the link between the ultimate causes (i.e. habitat or food availability) and the proximate factors of decline (i.e. breeding success or philopatry) (Kristin et al. 2000; Lepley et al. 2004; Kristin et al. 2007; Giralt & Valera 2007; Giralt et al. 2008). We contribute to these studies here identifying the return rates as the main responsible of the last ten years decline of this western European population.

Even though we can not distinguish the relative contribution of true mortality/survival and emigration/philopatry on the observed low return rates on our study population, it is interesting to mention some issues about both processes. Mortality is often reported as the most determinant parameter for population viability across bird species and other taxonomic groups (Heppell et al. 2000; Stahl & Oli 2006), and has been suggested as a possible key parameter beneath the historic decline of this shrike (Lefranc 1993; Kristín 2008). It is worth to say that it is one of the Palaearctic passerines which makes a longer migration (10.000 km two times per year) (Lefranc & Worfolk 1997), which suggests this species to be, for example, more sensitive to climate change mismatches (Both et al. 2006; Giralt & Valera 2007; Newton 2008). Therefore, high mortality rates may be likely to occur in this shrike compared to similar bird species, contributing to the decline in Spain and in other European populations.

Concerning the possible role of dispersal, Curnutt et al. (1996) showed that source-sink dynamics can explain variability at the periphery of a species range where population size is governed largely by migration/dispersal rather than by reproduction and survival. Giralt & Valera (2007) found a strong spatial correlation between southern France populations' sizes and an already extinct population of this shrike in Northeast Spain, suggesting that the same major factor/s was/were regulating in the same way those populations. Although the authors found a strong correlation between population fluctuations and climatic factors in the breeding areas (Giralt & Valera 2007), a shared dispersal/mortality mediated process could not be excluded as the responsible of such spatial autocorrelation.

Furthermore, density-dependence dispersal could have also been operating in our study population through an Allee effect, for example reducing site fidelity (and thus increasing emigration) as the population size decreased (Courchamp et al. 1999). We can not rule out that the observed low return rates were already the consequence of a positive density-dependent site fidelity to a breeding area that every year missed more birds. Courchamp et al (1999) suggested that when the fitness of a species is improved by conspecific proximity and facilitation (habitat copying, nest defence, probability of finding a mate, etc), it may suffer in low density populations. Facilitation is particularly determinant in colonial birds, where conspecific attraction plays an important role on the final balance between emigration and immigration (Serrano et al. 2004). The Lesser Grey Shrike may be potentially sensitive to density-dependent processes since it has some traits of a semi-colonial bird, pairs nesting often in clusters (Lefranc 1993; Kristin et al. 2000) and using conspecific information for nest-site selection (Hoi et al. 2011).

On the other side, we have assumed a null immigration rate in all of our viability analysis and isolation may be a too strong scenario to avoid local extinction, as predicted by metapopulation ecology (Hanski 1999). We are confident on this assumption, given the already observed genetic loss in our population (Kvist et al. 2011), the negligible immigration rate observed from ringed birds on the nearest and small (less than 10 breeding pairs) population located at 40 km, and on the marginal and distant (1500 km) position of the Spanish population in relation to the species strongholds in east Europe, the main potential source of birds. The crucial role of immigration on population regulation has been recently demonstrated for the ecologically similar Red-backed shrike (Schaub et al. 2013), and may be also determinant for our study species. For example, in Slovakia, Kristin et al. (2007) reported a similar return rate of adults (40% on males and 25% on females) that the one found in our study population, which we have seen that it is not enough to allow any population to be viable. Because the Slovak population was stable and healthy during that period (Kristin et al. 2000), this may indicate that immigration was high at that time on that central European population, compensating the observed low return rates. Indeed, after analysing the temporal pattern of nest-site re-use in the Slovak population, Kristin et al. (2007) also suggested that the strategy of dispersing over staying may be selected on that species. Therefore, apart from return rates, isolation and thus low immigration rate, has very likely played a strong role on the decline of the Spanish and other Lesser Grey shrike populations located at the western edge of the distribution area.

Finally, stochasticity has been often suggested (but rarely documented) as the last responsible of the extinction when populations reach a very low size (less than 20 pairs in our case), because any abnormal deviation from the mean of vital rates has a greater impact on small than on large populations (Hanski 1999). The sharp drop of breeding pairs between 2007 and 2008 (89% of marked birds did not return) and the subsequent strong female-biased sex ratio, may be a good example of how stochasticity can accelerate an extinction process of a small popualtion just because of a bias in the death distribution across genders, and altering the usual male-biased sex-ratio in shrikes (Lefranc & Worfolk 1997) and other small bird species (Dale 2001; Donald 2007).

Conservation implications

Our case study is an example in conservation biology of small populations, where conservation decisions are needed in the absence of enough information. Close monitoring arrived late (19 breeding pairs) for this shrike population because when a population reaches low numbers it is already difficult to correctly identify and reverse the effects of different limiting factors acting together, including stochasticity and Allee effects (Simberlof 1986; Caughley 1994; Hanski 1999; Reed et al. 2003). Furthermore, our study reveals that when strong conservation action started to be applied, the main Spanish population was already doomed to extinction without any change on return rates. This mismatch is partly explained because the first global assessment of the Spanish population was very recent (Giralt et al. 2010), the hope of finding more breeding sites existed, and it was uncertain to what extent the observed dynamics were the rule or an exception. Therefore, because urgency is a bad partner in conservation biology and time is needed to properly understand population dynamics (Reed et al. 2003), if possible, it is crucial to start monitoring species or populations when they still holds large numbers.

Another remarkable aspect of our study is that it identifies the predominant role of survival and/or dispersal rates above reproductive rates in the studied population. This distinction is crucial from a conservation point of view, since it conditions the strategy and success of any conservation project (Morris & Doak 2002). If management can only be applied locally on the breeding grounds while population's dynamics are mainly governed by other parameters than breeding rates, population decline it is likely to continue. In these situations, where local population's fate depends on a metapopulation, management should be applied at a larger scale, including the source populations and i.e. enhancing habitat connectivity to favour dispersal between sources and sinks (Hanski 1999; Channell & Lomolino 2000). Therefore, our results can be useful for other studies focused on threatened populations or species, and specifically for the remaining Lesser Grey Shrike populations in east Europe and Asia, where we strongly encourage the monitoring of the species and its vital rates, before the numbers reach the current low levels in west Europe.

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