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**Etude des paramètres de reproduction et de la
dynamique d'une population renforcée d'outardes
Houbara nord-africaines (*Chlamydotis undulata
undulata*) au Maroc**

Léo Bacon

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Léo Bacon

Le 15/12/2017

**Etude des paramètres de reproduction et de la dynamique d'une
population renforcée d'outardes Houbara nord-africaines
(*Chlamydotis undulata undulata*) au Maroc.**

Sous la direction de : **Alexandre Robert et Yves Hingrat**

JURY :

Alexandre Robert

Yves Hingrat

Daniel Oro

Vincent Bretagnolle

Jane Lecomte

Matthieu Guillemain

Maître de conférences, Muséum National d'Histoire Naturelle

RENECO International Wildlife Consultants . LLC.

Professeur, IMEDEA

Directeur de recherche, CNRS

Professeur, Université Paris Sud

Ingénieur, ONCFS

Directeur de Thèse

Directeur de Thèse

Rapporteur

Rapporteur

Examineur

Examineur

Résumé

En biologie de la conservation, les translocations (réintroductions ou renforcements) utilisent les lâchers d'individus pour restaurer des populations d'espèces ciblées. Cela implique que ces actions de translocation soient temporaires et conduites dans le but d'obtenir des populations stables et viables. Cependant, cet objectif est difficilement mesurable car il requiert le suivi de ces populations, réintroduites ou renforcées, qui sont des systèmes complexes caractérisés par des individus lâchés et des individus nés à l'état sauvage qui peuvent présenter des paramètres démographiques différents.

A travers cette thèse, nous avons étudié une population renforcée d'outarde Houbara nord-africaine (*Chlamydotis undulata undulata*) au Maroc. Cette population est renforcée via des lâchers réguliers d'individus produits en captivité. L'objectif est d'augmenter la taille de la population, pour établir une population viable et soutenable en adéquation avec la persistance de la fauconnerie traditionnelle. Cet objectif nécessite d'évaluer la capacité des individus lâchés à survivre et à se reproduire en milieu naturel et donc d'intégrer la population reproductrice sauvage. Nous avons ainsi évalué les paramètres de reproduction des outardes Houbara femelles lâchées et nées à l'état sauvage, afin d'étudier comment les renforcements affectent la dynamique de la population.

Dans un premier temps, nous avons analysé les performances reproductrices des femelles lâchées produites en captivité, en fonction de leur âge. La plupart des paramètres de reproduction étudiés montraient des variations en fonction de l'âge des femelles, variations comparables aux modèles qui caractérisent les populations de vertébrés sauvages. Ceci suggère que l'histoire de vie des femelles issues des translocations n'est pas affectée par les protocoles de lâcher.

Puis, nous avons évalué les performances reproductrices des femelles lâchées par rapport à celles de femelles nées à l'état sauvage. Nous avons observé de plus faibles performances reproductrices des femelles lâchées pour certains des paramètres de reproduction étudiés, constituant une forme au long terme de coût au lâcher. Ce coût au lâcher semble être en partie dépendant de la stratégie de lâcher (période de lâcher).

Nous nous sommes ensuite intéressés au lien entre environnement et performances reproductrices. En se basant sur un indice spatial de qualité d'habitat, nous avons exploré comment celui-ci était relié à la survie des nids. Nous avons observé un lien dynamique entre indice de qualité de l'habitat et survie des nids au sein de la saison de reproduction. Il semble donc qu'une utilisation statique de l'indice de qualité d'habitat ne permette pas de représenter la complexité des patrons démographiques et de leurs dynamiques au sein de la saison de reproduction.

Enfin, nous avons développé des modèles quantitatifs de viabilité des populations pour évaluer l'implication de la pression de chasse et de l'effort de renforcement sur la persistance de la population. Nos résultats indiquent que la population d'outarde Houbara nord-africaine n'est pas viable au long terme sans interventions de renforcement et que le déclin de la population n'est pas seulement causé par la chasse mais également par d'autres menaces. Par conséquent, le programme de renforcement apparaît ici comme un outil de conservation efficace pour préserver relativement rapidement l'espèce de l'extirpation locale, afin de pouvoir appréhender les principaux facteurs environnementaux menaçant la population.

Mots-clés : Démographie, Maroc, nids, outarde Houbara, reproduction, translocation

Abstract

In the field of conservation biology, conservation translocations (such as reintroductions and reinforcements) rely on the movement and release of individuals to restore populations of the concerned species. This implies that translocations are temporary actions conducted to reach a self-sustainable population. Yet, this objective is hardly assessed because it requires longitudinal monitoring of translocated populations, which are complex and unbalanced systems characterised by a mix of released and wild-born animals with potentially distinct and heterogeneous demographic rates.

In the present work, we studied a reinforced population of the threatened North-African Houbara bustard (*Chlamydotis undulata undulata*) in Morocco. Based on a captive breeding programme, the Houbara population is reinforced through the regular releases of captive-bred individuals. The objective is to increase the population size of the species throughout its range, to establish a viable and sustainable population in adequacy with the persistence of traditional Arab falconry hunting. This objective requires the assessment of the capacity of captive-bred individuals to survive and breed in the wild, and thus integrating the breeding population. As such, we intended to assess breeding parameters of females Houbara and to investigate how reinforcement actions influence the dynamics of the population.

At first, we studied how breeding performances of captive-bred females released in the wild vary as a function of their age. We observed that most breeding parameters exhibit age variations similar to patterns of variation generally observed in wild populations of vertebrates, suggesting that the life histories of translocated individuals are not strongly affected by translocation protocols.

Secondly, we assessed the breeding performances of captive-bred released females relative to wild-born females and release strategy. We observed lower breeding performances of released females for some breeding parameters, defined as a long term cost of release. Interestingly this cost of release appeared to be partly dependent on the release strategy (season of release).

Then, we assessed the relationship between environment and breeding performances. Based on a habitat suitability index, we investigated how this index was related to nest survival. We observed an intraseasonal dynamic relationship between habitat suitability and nest survival. This result underlines the idea that a static use of habitat suitability index, despite their sophistication, does not appear to reflect the complexity of demographic patterns and intraseasonal dynamics.

Finally, we developed quantitative population models to assess the involvement of hunting pressure and reinforcement effort to the persistence of the population. Our results indicate that the North-African Houbara bustard population is not viable without reinforcement interventions on the long run, and that the decline of the population is not only caused by hunting. Therefore the reinforcement programme appears as an efficient conservation tool to preserve the species from local extirpation before key environmental factors threatening the population can be adequately addressed.

Keywords: Demography, Morocco, Houbara bustard, nests, reinforcement, reproduction, translocation

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- Oral. Bacon, L., Hingrat, Y., Jiguet, F., Monnet, A.C., Sarrazin, F., Robert, A., 2016. Habitat suitability and demography, a time dependent relationship. *Young Natural History scientists Meeting*. Paris, France.

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Figure. Alexandre Robert et son valet me ramenant à ma condition de simple doctorant.

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Et comme disait Platon, «The end».

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Introduction

Les translocations

En écologie, les translocations sont définies comme des actions menées par l'homme visant à déplacer délibérément et intentionnellement des organismes vivants, issus de n'importe quelle source, et à les lâcher dans le milieu naturel (Ewen et al. 2012, IUCN 1987, 1998). Les actions de translocation peuvent avoir des objectifs multiples.

Certaines translocations sont par exemple motivées par des intérêts commerciaux et/ou récréationnels, comme les translocations d'espèces liées aux sports de pêche (Cambray 2003, Gozlan 2011) et de chasse (Champagnon et al. 2013). De nombreuses espèces exotiques sont introduites comme agents de contrôle biologique en agriculture (Simberloff & Stiling 1996) ou à des fins ornementales, comme c'est le cas pour de nombreuses espèces végétales (Starfinger et al. 2003).

D'autre part, des actions de translocation, dites conservatoires, visent à améliorer le statut de conservation de populations, d'espèces, voire d'écosystèmes. La première translocation conservatoire répertoriée date du début du 20^{ème} siècle. Elle concerne la translocation de bisons d'Amérique du Nord (*Bison bison*) dans une réserve établie en Oklahoma, Etats Unis d'Amérique (Kleiman 1989, Seddon et al. 2007).

On distingue deux types de translocations conservatoires, les actions de restauration des populations et les introductions conservatoires. Les translocations pour la restauration des populations sont les réintroductions et les renforcements de populations. L'objectif des réintroductions est le rétablissement de populations stables et persistantes d'une espèce dans son aire historique d'où elle a disparue (Ewen et al. 2012). Les réintroductions du vautour moine (*Aegypius monachus*) dans les Grands Causses en France (Mihoub et al. 2014) ou de l'oryx d'Arabie (*Oryx leucoryx*) en Oman (Spalton et al. 1999) sont des exemples parmi beaucoup d'autres. Les renforcements (également nommés suppléments) concernent la translocation d'individus dans une population conspécifique existante. L'objectif est de réduire les risques d'extinction par l'augmentation de la taille de la population, pour améliorer la croissance démographique, minimiser les risques de dépression de consanguinité en augmentant la diversité génétique (Ewen et al. 2012). On peut prendre en exemple le plan de renforcement de la population d'ours brun des Pyrénées (*Ursus arctos arctos*), par la translocation d'individus d'origine Slovène (Arquillière 1998).

Les introductions conservatoires sont des translocations intentionnelles d'organismes hors de leur aire de répartition historique. Les introductions conservatoires peuvent avoir un objectif de rétablissement de fonctions écologiques perdues. Un exemple controversé est l'idée d'introduction du lion (*Panthera leo*) en Amérique du Nord pour rétablir les fonctions écologiques des grands prédateurs du pléistocène (Donlan 2005). On retrouve aussi au sein des introductions conservatoires les colonisations assistées. Ces translocations visent à introduire une espèce dans un habitat favorable pour la protéger des menaces auxquelles elle peut faire face dans son aire de distribution naturelle (Hoegh-Guldberg et al. 2008).

La dichotomie des translocations entre intérêts conservatoires et non-conservatoires n'est cependant pas toujours aisée et une même translocation peut avoir différents objectifs. Un des exemples les plus probants est celui du renforcement de populations pour la chasse (populations exploitées) qui peut présenter à la fois des intérêts conservatoires et commerciaux/récréationnels. Ces renforcements peuvent, dans un but conservatoire, viser au maintien, à l'accroissement et/ou au rétablissement de populations viables et stables soumises aux prélèvements par l'intégration d'individus lâchés à la population sauvage. A l'opposé, ils peuvent être motivés par l'accroissement dans le temps, dans l'espace et de manière quantitative, des opportunités de chasses (Champagnon 2011, Sokos et al. 2008). Dans certains cas, les renforcements permettent la préservation de populations sauvages par d'importants lâchers d'individus destinés à des prélèvements immédiats, qui absorbent tout ou partie de la pression de chasse (Champagnon et al. 2009, Sokos et al. 2008). Dans de nombreux cas ces actions de renforcement se basent sur des programmes d'élevages *ex-situ* (Champagnon et al. 2013, Sokos et al. 2008).

Translocations et élevages ex situ

Les individus utilisés pour les translocations peuvent provenir de populations sauvages ou de programmes d'élevage *ex-situ*. Lorsque le risque d'extinction est élevé, la préservation de certaines espèces peut nécessiter la mise en place d'un élevage conservatoire. Les conditions de captivité présentent un environnement stable et sécurisé (absence de prédateurs, soins vétérinaires, ressources alimentaires *ad libitum*) qui permet d'augmenter les performances démographiques des individus (survie, productivité) et favorise donc la persistance de l'espèce au long terme (Ricklefs and Scheurlein 2001). Par ailleurs, en comparaison de translocations d'individus issus d'une population sauvage source, les élevages *ex situ* nécessitent généralement des prélèvements moindres d'individus, afin de constituer la population captive reproductrice initiale. Ceci permet (dans la mesure où la reproduction en

captivité est achevée) de développer des actions de translocations pour des espèces dont les populations naturelles sont en effectifs réduits et dont les prélèvements réguliers pourraient accentuer leur probabilité d'extinction. Dans le cadre de translocations liées à la chasse, les élevages ex-situ sont souvent nécessaires car les effectifs sauvages ne permettent pas de répondre aux attentes, demandes et objectifs de renforcement et de prélèvement (Champagnon 2011). Cependant, la reproduction d'individus en captivité est souvent difficile et présente de nombreux risques (Conway 1986, Snyder et al. 1996). Les programmes de reproduction en captivité se basent généralement sur un lot d'individus fondateurs réduit. Ces faibles tailles de populations, additionnées aux conditions de captivité, nécessitent une gestion génétique stricte des lots d'individus reproducteurs. Une mauvaise gestion génétique des stocks d'individus reproducteurs peut provoquer une augmentation des taux de consanguinité, notamment lorsque qu'il s'agit de petits effectifs, provoquant une diminution de la valeur sélective de la population captive par des phénomènes de dépression de consanguinité (Christie et al. 2012, Snyder et al. 1996). Les phénomènes de dérive génétique peuvent conduire à la fixation et l'accumulation d'allèles partiellement délétères (Lynch & O'hely 2001). A cela s'ajoute la perte de diversité génétique (Weeks et al. 2011) et des adaptations génétiques aux milieux captifs (domestication, Christie et al. 2012, Frankham 2008, Lynch & O'hely 2001). Ces caractéristiques génétiques des individus, liés à la captivité, peuvent s'avérer délétères en conditions naturelles et affecter négativement la dynamique des populations issues de translocations (Robert 2009). Araki et al. (2007) ont montré que les effets génétiques liés à la domestication réduisaient la capacité de reproduction de salmonidés lâchés en milieu naturel de 40% par génération passée en élevage. Par ailleurs, différents travaux ont mis en évidence un plus faible succès des translocations se basant sur des populations captives que sur des populations sources sauvages (Griffith et al. 1989, Jule et al. 2008, Wolf et al. 1996).

Risques, menaces et conflits liés aux translocations

Même à portée conservatoire, les translocations d'espèces animales et végétales présentent des risques pour les populations et écosystèmes ciblés ainsi que de potentiels conflits socio-économiques.

La translocation de nouveaux individus ou de nouvelles espèces peut perturber les processus écologiques, la dynamique et la stabilité des populations et écosystèmes récepteurs. Selon Stringer & Gaywood (2016), la réintroduction du castor (*Castor fiber*) en Ecosse pourrait impacter négativement certains habitats forestiers et espèces végétales d'intérêt conservatoire qui les constituent. Les introductions d'espèces, dans le cadre de colonisation assistées, sont

largement discutées et débattues car elles présentent un risque d'introduction d'espèces au potentiel invasif (Mueller & Hellman 2008, Seddon et al. 2009), d'introduction de pathogènes (Griffith et al. 1993, Snyder et al. 1996), etc.

Dans le cas des renforcements, la transmission de pathogènes et parasites représente une menace de par les contacts directs existant entre les individus lâchés et les individus sauvages. Aux Etats Unis, de nombreuses populations de dindon sauvage (*Meleagris gallopavo*) sont infectées par *Plasmodium kemp*, qui résulterait de la translocation d'oiseaux infectés (Castle & Christensen 1990).

Les translocations d'individus présentent des risques de modifications génétiques des populations cibles et espèces proches à travers des phénomènes d'hybridation, d'introgession génétique intra et inter-spécifique (transferts de gènes entre populations/espèces proches, Barbanera et al. 2010, Weeks et al. 2011). En Europe, la production et le lâcher de perdrix hybrides (perdrix choukar *Alectoris chukar* × perdrix rouge *Alectoris rufa*), destinées à la chasse, a causé l'introgession d'allèles de la perdrix choukar dans les populations sauvages de perdrix rouge (Barbanera et al. 2010). L'introgession d'allèles qui ne sont pas adaptés aux conditions locales peut engendrer une diminution de la valeur sélective des populations natives et par la suite augmenter les risques d'extinction des populations. Ce pourrait être le cas pour la truite fardée (*Oncorhynchus clarkii lewisi*), en Amérique du Nord, dont l'hybridation avec la truite arc-en-ciel introduite (*Oncorhynchus mykiss*) produit des individus fertiles mais avec un succès reproducteur amoindri (Muhlfeld et al. 2009). Plus encore, ces hybridations et introgessions peuvent amener une perte de diversité génétique des populations natives et potentiellement à leur extinction génétique (Rhymer & Simberloff 2009). En Ecosse, l'intégrité génétique des populations de cerfs élaphe (*Cervus elaphus*) est menacée par l'introgession d'allèles issus de son hybridation avec le cerf sika (*Cervus nippon nippon*) introduit au début du 20^{ème} siècle (Abernethy 1994).

Les translocations d'espèces peuvent aussi être source de conflit avec l'Homme par les perturbations qu'elles provoquent sur certains services écosystémiques et activités économiques (Stahl et al. 2001).

Enfin, dans le cadre de renforcement de populations pour la chasse, les actions de renforcement peuvent s'avérer délétères pour la persistance des populations sauvages si elles sont prétextes à une hausse démesurée de la pression de chasse et à la négligence d'autres actions de conservation (Sokos et al. 2008).

Mise en place d'un programme de translocation

Avant même la mise en place d'un programme de translocation, il est nécessaire d'évaluer s'il s'agit de la méthode la plus appropriée à appliquer pour répondre aux objectifs. Dans un cadre conservatoire, la restauration d'habitats dégradés ou la mise en place d'aires protégées peuvent se révéler plus efficaces que des actions de translocation (IUCN 2013).

La mise en place d'un programme de translocation nécessite d'avoir des connaissances préalables de la biologie et écologie de l'espèce ainsi que de son statut de conservation (IUCN 2013). Ces connaissances permettront de développer les stratégies de translocation les plus adaptées à l'espèce/population. Le statut conservatoire de l'espèce sera notamment un argument clé dans le choix des populations sources, captives ou sauvages. Dans le cas où le programme de translocation doit se baser sur des élevages *ex situ*, le choix des individus fondateurs devra se faire en considération de la diversité génétique de l'espèce et/ou des particularités génétiques des populations réceptrices dans le cas de renforcement. La prise en compte des besoins biotiques et abiotiques de l'espèce est indispensable dans la détermination des habitats qui apporteront les conditions nécessaires à la persistance de l'espèce (Ewen et al. 2012, Seddon 2013). La caractérisation de ces habitats par le développement de cartes et informations spatiales produit des outils décisionnels qui permettent de définir et prédire les zones les plus favorables pour assurer et maximiser le succès des translocations (Guisan et al. 2013, Hodgson et al. 2009, Monnet 2014). Les stratégies de lâcher (nombre d'individus, sexes et âges des individus lâchés, période de lâcher, etc.) devront aussi répondre aux caractéristiques biologiques et écologiques de l'espèce et aux objectifs de translocation.

Les risques pour les populations et écosystèmes récepteurs, mentionnés plus haut, doivent être quantifiés au préalable et minimisés autant que possible (IUCN 2013). La vaccination des individus et des phases de quarantaines pourraient réduire la probabilité d'introduction de nouveaux pathogènes dans le milieu récepteur (Bailey et al. 2000, Cunningham 1996).

Le succès d'un programme de translocation ne peut se faire, par ailleurs, sans avoir identifié et écarté au préalable les facteurs qui menacent la persistance de l'espèce dans les zones d'intérêt (IUCN 2013). Dans certains cas, la suppression des menaces et la réussite du programme passe par l'acceptation de celui-ci par les communautés humaines locales. Il s'agit d'une problématique récurrente pour des programmes de réintroduction de grands carnivores et d'espèces pouvant causer des conflits culturels et socio-économiques (Stahl et al. 2001).

La mise en place d'un programme de translocation est un processus long et coûteux, et l'ensemble des directives mentionnées (listées par l'IUCN, « *International Union for Conservation of Nature* », IUCN 2013) sont rarement toutes respectées face aux menaces qui pèsent sur les populations et qui nécessitent des actions concrètes et immédiates.

Evaluation du succès d'un programme de translocation

Le succès d'un programme de translocation est difficilement quantifiable (Ewen et al. 2008). Dans leur revue, Fischer and Lindenmayer (2000) ont montré que pour 47% des réintroductions étudiées, la réussite ou non du programme était inconnue. De manière générale, le succès au long terme d'une translocation peut se caractériser par la capacité des individus issus de la translocation à survivre et à produire des descendants viables et productifs permettant la stabilité et la persistance de la population sans actions de translocations additionnelles (Ewen et al. 2012, IUCN 2013).

L'évaluation du succès d'un programme de translocation s'effectue par des suivis individuels post-translocations. La mise en place de ces suivis doit avoir des objectifs précis pour répondre à des problématiques de conservation des populations cibles et améliorer les stratégies de translocation (« *adaptive management* », Armstrong & Seddon 2008, Ewen & Armstrong 2007). Sarrazin et al. (1996) ont montré que dans le cadre du programme de réintroduction du vautour fauve (*Gyps fulvus*) dans le massif central, les individus lâchés juvéniles avaient un succès reproducteur plus élevé que les individus lâchés à l'âge de 2 ans et plus. L'étude des performances démographiques des individus issus des translocations procure les premiers critères d'évaluation du succès de translocation. L'observation d'individus qui persistent et se reproduisent en milieu naturel peut être considérée comme un indice de succès car ce sont les critères fondamentaux pour l'établissement et la persistance d'une population au long terme (Bertolero & Oro 2009). Les suivis des populations soumises à des programmes de translocation ont permis de mettre en évidence, dans de nombreux cas, les faibles performances démographiques des individus lâchés. Tavecchia *et al.* (2009) ont montré une forte mortalité consécutive au lâcher de foulques à crête (*Fulica cristata*). Le programme de réintroduction du vautour fauve (*Gyps fulvus*) dans les Causses a mis en évidence de plus faibles performances reproductrices des individus lâchés adultes que des individus nés à l'état sauvage (Sarrazin et al. 1996). Enfin de nombreux programmes de renforcement de populations de galliformes à des fins cynégétiques ont montré de plus faibles performances reproductrices des individus lâchés nés en captivité en comparaison des individus nés à l'état sauvage (Buner et al. 2011, Leif 1994, Musil & Connelly 2009). Ces

plus faibles performances démographiques sont souvent définies comme le coût au lâcher. Le terme de coût au lâcher est communément utilisé pour présenter les aspects de survie au court terme des individus issus de translocation (Tavecchia et al. 2009). Nous avons préféré ce terme à celui d'effet post-lâcher (Ewen et al. 2012) pour qualifier dans son ensemble les plus faibles performances démographique des individus issus de translocations (que ce soit sur le court ou long terme après le lâcher) car il permet de mettre en avant les difficultés et défis liées aux translocations.

Ce coût au lâcher s'explique par l'interaction du génotype et phénotype des individus issus des translocations avec leur nouvel environnement. Le manque d'expérience des individus issus de la translocation dans leur nouvel environnement (Tavecchia et al. 2009), les conditions d'élevages et de lâcher affectant les conditions des individus (santé, physiologie et comportement, Champagnon et al. 2012, Dickens et al. 2010), ainsi que des adaptations génétiques, particulièrement pour les individus produits en captivité, peuvent se révéler délétères une fois en milieu naturel (Araki et al. 2007, Christie et al. 2012). Ces coûts au lâcher peuvent se mesurer en examinant les caractères d'intérêts des individus lâchés en fonction de différentes stratégies de translocations (e.g. selon l'âge au lâcher, Sarrazin et al. 1996), par la mise en perspective des caractères des individus lâchés par rapport aux caractères des individus issus de populations sources et/ou cibles (e.g. comparaison entre individus nées à l'état sauvage et en captivité, Brown et al. 2006) ou par les comparaisons des caractères à différentes échelles temporelles (e.g. la survie des individus post-lâcher par rapport à la survie des individus au long terme, Tavecchia et al. 2009).

La collecte de ces données démographiques permet par la suite d'établir des modèles de dynamique et viabilité des populations. Ceux-ci permettent de quantifier les tendances de la population ainsi que sa probabilité d'extinction (Sarrazin 2007, Robert et al. 2015a). Ces données quantitatives mises en parallèle des critères de classification des espèces menacées de la liste rouge de l'IUCN (IUCN 2012, Robert et al. 2015a), permettent d'adapter les stratégies de conservation de l'espèce (Armstrong et al. 2007) et d'évaluer le succès des translocations. Cependant, les populations restaurées par translocation sont des systèmes complexes et hétérogènes. Pour décrire leur dynamique au long terme et donc leur viabilité, il est nécessaire :

- (1) de prendre en compte les effets confondants qui existent sur la démographie de l'espèce, tels que les aspects temporels et âge dépendants,

- (2) de caractériser l'hétérogénéité démographique qui découle des stratégies de translocations, tels que l'origine des individus (nés à l'état sauvage ou issus de translocation),
- (3) d'identifier les variations spatiales et temporelles qui pourraient influencer sa démographie.

Modèle d'étude : Une population renforcée d'outardes Houbara nord-africaine au Maroc.

Taxonomie

L'outarde Houbara est un nom vernaculaire qui désigne deux espèces du genre *Chlamydotis*, de la famille des Otididae :

- *Chlamydotis macqueenii*, encore nommée outarde de Macqueen ou outarde Houbara asiatique, dont l'aire de répartition se trouve dans les régions steppique du Moyen Orient et d'Asie Centrale depuis la péninsule du Sinaï jusqu'à l'Est de la Mongolie (Fig. 1).
- *Chlamydotis undulata*, qui se subdivise en deux sous-espèces, *C.u.fuertaventurae*, l'outarde Houbara endémique des îles Canaries et *C.u.undulata*, l'outarde Houbara nord-africaine, que l'on retrouve dans les steppes semi-désertiques d'Afrique du Nord, depuis le Nord de la Mauritanie jusqu'à l'Ouest du Nil (Fig. 1).

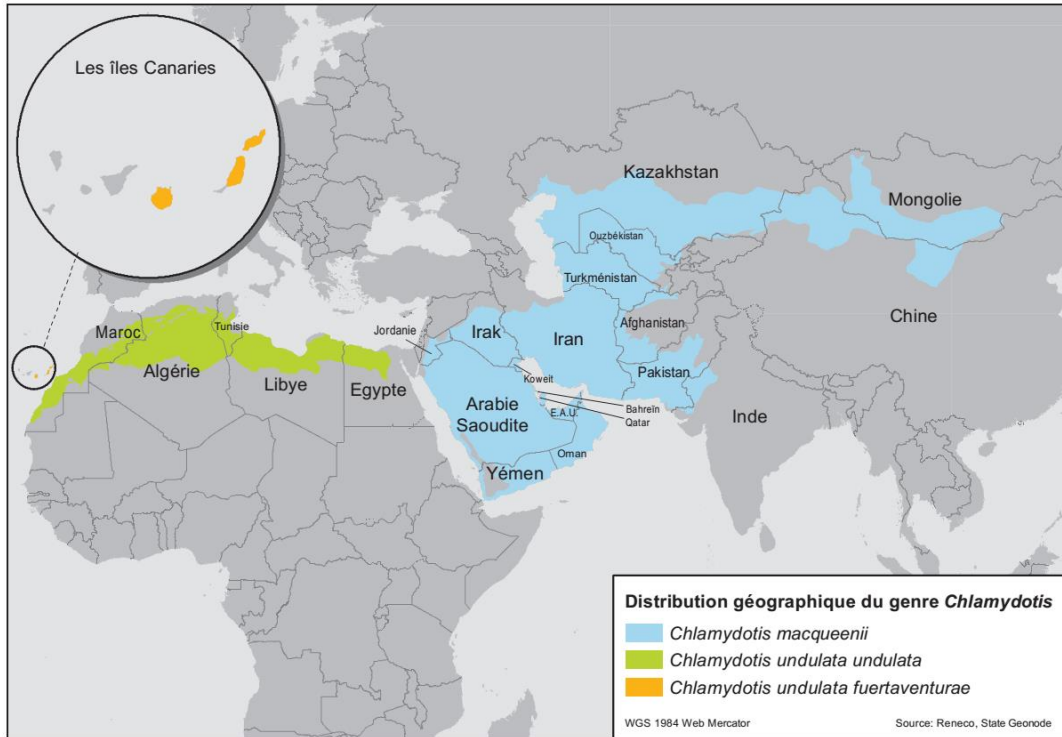


Figure 1. Distribution géographique du genre *Chlamydotis*

Auparavant classées comme sous-espèces, la distinction spécifique entre *C.macqueenii* et *C.undulata* ne s'est faite que récemment sur des critères génétiques et comportementaux (Gaucher et al. 1996, Knox et al. 2002).

Les travaux de cette thèse concernent uniquement l'outarde Houbara nord-africaine (*Chlamydotis undulata undulata*).

Biologie et écologie

L'outarde Houbara nord-africaine (nommée outarde Houbara ci-après), est un oiseau de taille moyenne (55-65 cm de longueur et 135-170 cm d'envergure, Saint Jalme & van Heezik 1996) présentant un dimorphisme sexuel avec des individus mâles plus grands et plus gros que les individus femelles (en milieu naturel, en moyenne 1900 g pour les mâles et 1300 g pour les femelles, ECWP données non publiées). Elle présente un plumage cryptique lui permettant de se fondre dans les paysages steppiques d'Afrique du Nord. On observe sur les flancs et à la base du cou des plumes érectiles noires et blanches généralement plus longues chez les mâles que chez les femelles.

L'outarde Houbara se retrouve dans les steppes semi-désertiques d'Afrique du Nord, sur le pourtour Nord du Sahara en dessous de l'isohyète 250 mm. Les habitats sont caractérisés par une végétation basse et éparse. Sur les hauts plateaux de l'Oriental marocain, l'outarde

Houbara se retrouve dans les regs et plaines aux sols riches en limon et argiles composés d'espèces végétales telles que *Stipa tenacissima*, *Artemisia herba alba* ou encore *Hamada spp.* (Hingrat et al. 2004). La production primaire et secondaire y est largement dépendante des précipitations locales et saisonnières qui sont irrégulières (Gamoun 2016, Warner 2004).

A l'échelle du paysage, ergs, montagnes et rivières permanentes sont des facteurs limitants de la distribution de l'espèce (Hingrat et al. 2008). Il a été montré que l'outarde Houbara évite les milieux anthropisés (Hingrat et al. 2008).

Chez l'outarde Houbara, l'exploitation de l'habitat est différentielle en fonction du sexe et varie selon un cycle annuel (Hingrat et al. 2007a). Cette exploitation différentielle de l'habitat est une conséquence directe du système de reproduction et d'appariement de l'outarde Houbara ainsi que de la dynamique de disponibilité des ressources (Hingrat et al. 2005, 2008).

L'outarde Houbara est une espèce polygyne avec un système d'appariement de type « lek diffus » (Hingrat et al. 2005, 2008). La saison de reproduction s'étend de début janvier à fin juin (Fig. 2). A partir de début janvier les mâles s'établissent sur leurs sites de parade. Ils ne prennent part à la reproduction que par la fécondation des femelles. Ces sites de parade sont agrégés spatialement, si bien que les domaines vitaux des mâles se chevauchent, sans monopolisation des ressources trophiques. Ces agrégations de sites de parades sont définies par le terme de « lek » (Bradbury 1983). Pour des espèces à leks « classiques », les sites de parades sont disposés à quelques mètres les uns des autres (Bradbury 1983). Pour l'outarde Houbara, la distance moyenne entre deux sites de parades d'un même lek est de 550 mètres (Hingrat et al. 2008). On qualifie alors ce système d'appariement de « leks diffus ». Les sites de parades sont des milieux ouverts à faible couverture végétale dans des zones surélevées. Ils favorisent la capacité des mâles à parader, à détecter et à être détectés par leurs conspécifiques (Hingrat et al. 2007a). On retrouve à la périphérie de ces sites ouverts des zones inondables au couvert végétal plus important, apportant les ressources trophiques nécessaires à leur alimentation (Hingrat et al. 2007a, 2008). La parade nuptiale du mâle est composée de signaux visuels et acoustiques complexes. Elle se caractérise par des courses frénétiques durant lesquelles les plumes blanches ornementales du cou se dressent, lui donnant une allure de boule blanche très distinctive (Fig. 3), ainsi que des phases de « booming » où le mâle émet des signaux sonores graves (les « booms », Cornec et al. 2014). Les mâles commencent à s'installer sur un site de parade et à parader entre l'âge de 2 et 4 ans. Ils sont généralement fidèles à leur site de parade pendant et entre les saisons de reproduction.

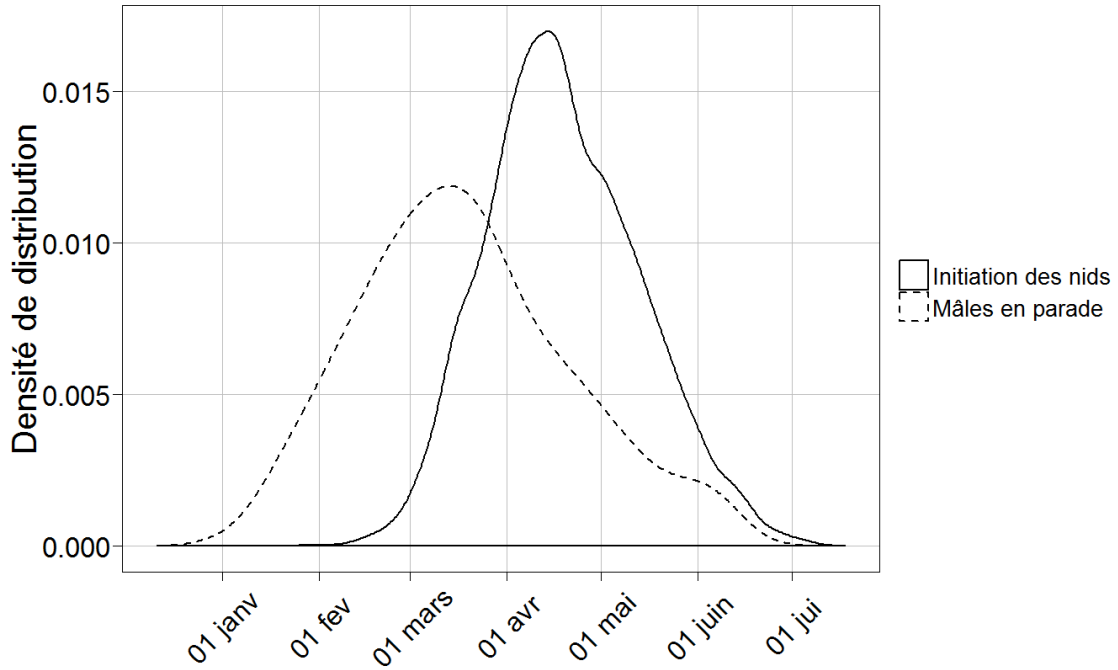


Figure 2. Densité de distribution de l'activité de parades et de nidification de l'outarde Houbara dans l'Oriental marocain. Données issus des moyennes bi-mensuelles de recensements de mâles en parades entre 2006 et 2014 et des dates de découverte des nids entre 2002 et 2016.



Figure 3. Outarde Houbara mâle en phase de parade nuptiale.

L'outarde Houbara est une espèce gynéparentale. Cela signifie que seule la femelle prend part à l'incubation des œufs et à l'élevage des poussins. Les femelles commencent à se reproduire entre 1 et 4 ans. Les femelles visitent les mâles uniquement pour la copulation et la fécondation de leurs œufs. Les premiers nids sont initiés entre mi-février et début mars et ce jusqu'à fin juin. Le pic d'activité de nidification oscille entre début et fin avril selon les

saisons (Fig. 2). La période de nidification est donc relativement longue. Il a été montré que les nids ont une distribution agrégative et sont localisés à la périphérie des leks. Cette distribution pourrait être expliquée par la préférence des femelles pour certains sites de nidification, par des effets d'attraction conspécifique ou des comportements de copiages entre femelles (Hingrat et al. 2008). Les femelles privilégient les habitats hétérogènes alliant lignes de drainages et zones à haut couvert végétal (Hingrat et al. 2007a, 2008). Ces habitats hétérogènes favoriseraient la capacité des femelles et de leur progéniture à se dissimuler face aux prédateurs tout en offrant les ressources nécessaires à leur alimentation. Les œufs sont pondus à même le sol sur une surface plane (Fig. 4, 5). Le nid se présente sous la forme d'une cuvette plus ou moins prononcée en fonction du substrat (Fig. 4). Les nids sont souvent disposés à proximité de buissons et de végétation basse, ce qui permettrait d'aider à la régulation de la température et de la perte en eau des œufs, grâce à l'ombre et à la protection contre le vent (Hingrat et al. 2008). Par ailleurs les femelles évitent de faire leur nid dans des oueds et cours d'eau asséchés car ils sont privilégiés par les prédateurs tels que le renard roux (*Vulpes vulpes*) pour se déplacer et rechercher la nourriture et car les pluies et écoulement pourraient emporter les œufs (Hingrat et al. 2008). Les femelles ne semblent pas présenter une fidélité intra et interannuelle marquée à un site de ponte spécifique (ECWP données non publiées). Des femelles ont été observées sur des sites de pontes distants de plusieurs dizaines, voire centaines de kilomètres entre années. Pour un nid, une femelle pond communément 2 à 3 œufs à 2.5 jours d'intervalle (Gaucher 1995). Les pontes de 1 et 4 œufs sont plus rares. Du parasitisme de ponte intraspécifique (stratégie de reproduction alternative) a déjà été observé chez l'outarde Houbara (Lesobre et al. 2010). Les auteurs suggèrent que ce comportement serait opportuniste, mais les mécanismes régulant son expression (conditions environnementales, densités, etc.) restent inconnus. Les œufs sont ovales. Ils présentent un panel de couleur allant du brun au vert ocre et sont tachetés de brun sombre sur tout ou partie de leur surface. De par leur couleur, les œufs sont particulièrement cryptiques et difficilement dissociables de leur substrat. Une fois la phase de ponte terminée la femelle incube les œufs en moyenne 23 jours. En cas d'échec de la ponte, la femelle initie communément une ponte de remplacement (jusqu'à 5 pontes observées dans la nature pour une femelle au sein d'une même saison de reproduction). La prédation des œufs est la principale cause d'échec des nids d'outarde Houbara (voir Méthodes - Suivi des nids avec pièges photographiques). L'éclosion des œufs est synchrone (l'intervalle de temps d'éclosion entre le premier et le dernier œuf ne dépasse pas 24h, ECWP données non publiées).

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Figure 4. Nid d'outarde Houbara.



Figure 5. Femelles outardes Houbara sur leurs nids.

Les poussins sont nidifuges. Cela signifie qu'ils quittent le nid peu de temps après l'éclosion du dernier œuf. Ils sont nourris par la femelle pendant les dix premiers jours qui suivent l'éclosion, principalement avec des arthropodes et de petits vertébrés (Fig. 6). Pendant les premières semaines de vie, les poussins se fient à leur plumage cryptique (Fig. 7) et leur capacité à rester immobile pour échapper aux prédateurs. Au fil des semaines, ils gagnent en indépendance et se déplacent plus aisément. Ils peuvent effectuer des premiers vols courts au

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bout de 3 à 5 semaines, mais restent avec la femelle jusqu'à deux à trois mois après l'éclosion (Hardouin et al. 2012). Cette période est cruciale car elle est considérée comme la phase d'apprentissage au cours de laquelle les poussins vont acquérir de l'expérience par le temps passé avec la femelle. Cette période d'élevage peut s'étendre jusqu'à début septembre.



Figure 6. Femelle outarde Houbara revenant au nid où se trouve un poussin.



Figure 7. Nid d'outarde Houbara avec un poussin et un œuf.

Consécutivement à cette période d'élevage suit une dispersion natale des juvéniles plus importante chez les mâles que chez les femelles (Hardouin et al. 2012). Ceci est en accord avec d'autres espèces d'outardes présentant un système d'appariement en leks (Martín et al. 2008).

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En dehors de la période de reproduction, les mâles sont majoritairement sédentaires et restent en périphérie de leur site de parade. Ils continuent ainsi à exploiter les différents habitats et ressources de leur zones de reproduction tout en élargissant leur aire de prospection alimentaire (accroissement du domaine vital) en raison de la diminution des ressources en automne et en hiver (Hingrat et al. 2004, 2007a). Chez les femelles, les stratégies sont plus variées. Si certaines sont sédentaires, beaucoup se déplacent vers de nouvelles zones en raison de la forte baisse de l'abondance des ressources trophiques à la fin de la saison de reproduction (Hingrat et al. 2007a). Les domaines vitaux sont ainsi plus importants et multimodaux (Hingrat et al. 2004). En dehors de la saison de reproduction les ressources ne sont pas seulement moins abondantes, mais aussi agrégées (hétérogénéité de la distribution des ressources entre les habitats, Hingrat et al. 2007b) favorisant le regroupement des oiseaux. Des groupes composés d'individus mâles, femelles et juvéniles se forment. Ces regroupements permettent une meilleure détection des prédateurs, ce qui pourrait être un avantage non négligeable pour les juvéniles.

Le régime alimentaire de l'outarde Houbara est généraliste et opportuniste (Bourass et al. 2012a). Il est le reflet de la disponibilité et de l'abondance des ressources trophiques (Bourass et al. 2012b). Pendant la saison de reproduction, lorsque les ressources en arthropodes sont abondantes et leur distribution homogène entre les habitats, la fraction animale dans le régime alimentaire est dominante (Bourass et al. 2012b, Hingrat et al. 2007b). Ce régime alimentaire permet de répondre aux importants besoins énergétiques liés à l'investissement dans la reproduction (parade, nidification et élevage des poussins). Cette fraction animale est principalement composée d'invertébrés et varie selon les émergences des différentes espèces (Bourass et al. 2012b). On retrouve une forte occurrence de coléoptères et hyménoptères (Formicidae) dont les pics d'abondance se retrouvent aux alentours de mai-juin selon les saisons (Hingrat et al. 2007b). Hors période de reproduction, lorsque les ressources animales se font plus rares, le régime alimentaire de l'outarde est principalement composé de végétaux (66% du régime alimentaire, Bourass et al. 2012a). L'espèce est un bon voilier, mais privilégie la marche et la course lors de ses déplacements et de sa prospection alimentaire. L'activité alimentaire se déroule en grande partie à l'aube et au crépuscule (Jacquet & Launay 1997).

Menaces et conservation

Il n'existe pas d'estimation précise des effectifs d'outardes Houbara à l'échelle de son aire de distribution. Cependant, il est considéré, par avis d'experts, que les populations ont décliné

d'environ 25% entre 1980 et le début des années 2000 (Birdlife International/IUCN 2016). L'outarde Houbara porte un statut d'espèce gibier emblématique auprès des chasseurs et fauconniers de la péninsule Arabe (Bailey et al. 1988, Goriup 1997). L'activité cynégétique non contrôlée ainsi que sa modernisation (mécanisation des moyens de transports, utilisation d'armes à feu, de GPS) au cours des dernières décennies ont joué un rôle majeur dans le déclin de l'espèce (Bailey et al. 1988, Goriup 1997). A cela s'ajoute le braconnage alimenté par la demande d'oiseaux pour l'entraînement des faucons (Bailey et al. 2000). Les dégradations et pertes d'habitats liées à l'intensification des activités pastorales (forte pression de pâturage des élevages ovins et caprins), et aux phénomènes de désertification qui en découlent, pourraient aussi être des facteurs expliquant la diminution de la distribution de l'espèce en Afrique du Nord (Chammem et al. 2003, Le Cuziat et al. 2005). Enfin les phénomènes globaux pourraient aggraver davantage l'état des populations. Il a été montré que les changements climatiques pourraient fortement modifier la structure des communautés de plantes dans les steppes utilisées par les outardes Houbara (Frenette-Dussault et al. 2013). Ceci accentuerait les processus de désertification, diminuant d'avantage la disponibilité de la niche écologique de l'espèce (Monnet 2014).

L'outarde Houbara est listées « Vulnérable » sur la Liste rouge de l'IUCN (Birdlife International/IUCN 2016). Les espèces listées vulnérables sont considérées comme faisant face à un haut risque d'extinction dans la nature (IUCN 2012). L'espèce est inscrite dans l'annexe I de la Convention de Bonn. Cette annexe inclut les espèces qui risquent l'extinction sur tout ou partie de leur aire de répartition. Cette annexe interdit tout prélèvement de spécimens (hors dérogation à des fins scientifiques et de conservation). Enfin, l'outarde Houbara se trouve dans l'annexe I de la Convention sur le commerce international des espèces de faune et de flore sauvages menacées d'extinction (CITES). L'annexe I comprend les espèces les plus menacées de toutes les espèces animales et végétales couvertes par la CITES. Le commerce de spécimens sauvages est interdit au niveau international, sauf cas exceptionnels.

L'Emirates Center for Wildlife Propagation

A l'initiative du Sheikh Zayed Bin Sultan Al Nahyan, pour répondre au déclin des populations et aux hauts risques d'extinction de l'outarde Houbara, l'Emirates Center for Wildlife Propagation (ECWP) a été créé en 1995 dans l'Oriental marocain (Fig. 8) et est aujourd'hui l'un des programmes phare de « l'International Fund for Houbara Conservation » (IFHC,

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www.houbarafund.org). L'objectif de l'ECWP est de rétablir des populations stables et viables d'outardes Houbara, en adéquation avec la persistance de la fauconnerie traditionnelle (Lacroix et al. 2003). Pour appliquer cet objectif de conservation, l'ECWP se base sur un élevage conservatoire (élevage *ex situ*) et un programme de renforcement des populations sauvages (lâchers d'oiseaux issus d'élevage en milieu naturel), combinés à des programmes de recherches et une gestion cynégétique des populations. L'élevage conservatoire est basé sur des individus fondateurs issus du milieu naturel, via différentes campagnes de collecte d'œufs en Algérie (1986-1987) et au Maroc (1996-1997, 2002-2009 et 2015-2016). Les individus sont reproduits en captivité par insémination artificielle (Saint-Jalme et al. 1994). Une gestion génétique des stocks est mise en place pour harmoniser la contribution génétique des individus fondateurs et éviter la consanguinité (Lesobre 2008) et respecter au mieux les directives IUCN d'élevage conservatoire (IUCN 2013). Une part des individus issus de l'élevage est par ailleurs intégrée au programme d'élevage pour renouveler le stock d'individus reproducteurs captifs. L'élevage conservatoire est mis à profit pour développer des questions de recherches fondamentales et liées à la conservation *in et ex situ*, à la sélection sexuelle, à la reproduction et aux effets de senescence sur les traits reproducteurs (Chantepie et al. 2015, Chargé et al. 2014, Loyau & Lacroix 2010, Preston et al. 2015).

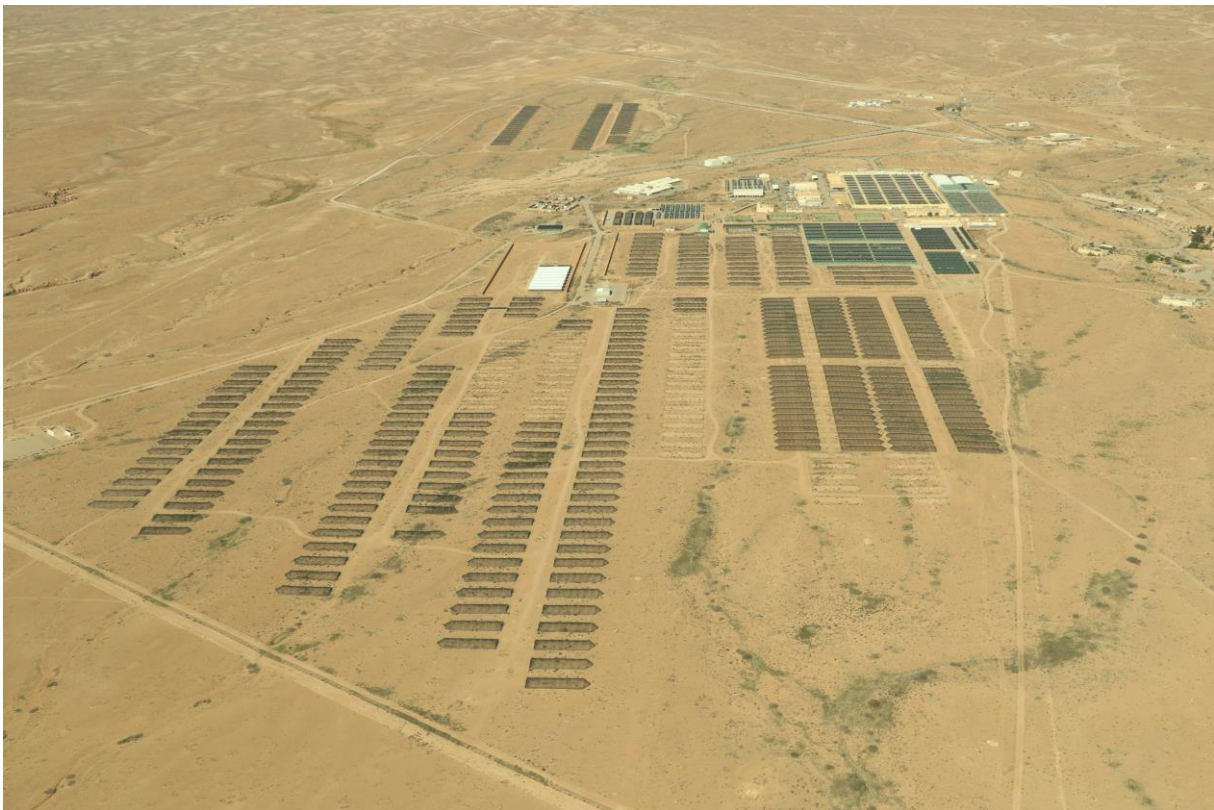


Figure 8. Station ECWP de Missouri, dans l'Oriental marocain.

Au total entre 1996 et 2016 plus de 108 000 oiseaux produits en captivité ont été destinés aux renforcements via leur lâché en Afrique du Nord (voir détails dans Chapitre 1 et 2). Les renforcements ont été réalisés en grande partie dans les aires d'interventions de Tata et de l'Oriental marocain (Fig. 9). Dans l'Oriental marocain, aire d'intervention principale de l'ECWP, le nombre d'oiseaux lâchés a progressivement augmenté au cours des années (de 28 en 1996 à 9084 en 2016, voir « Supplementary materials » - Chapitre 2), avec une augmentation du nombre de sites de lâcher et une diminution du nombre d'oiseaux par sites de lâcher (Hardouin et al. 2014). Le nombre d'oiseaux par site de lâcher varie entre sites (de 4 à 498 avec une médiane à 18). Les oiseaux sont lâchés en moyenne à 6 mois \pm 3 (écart-type) à l'automne (août à décembre) et 9 \pm 1 mois au printemps (février à mai). Depuis 2003, des oiseaux sont aussi lâchés à l'âge de 3 \pm 0.6 mois en juin. Tous les oiseaux lâchés sont marqués, soit d'une bague à la patte gauche soit d'un transpondeur sous-cutané (RFID 100 TROVAN, voir méthodes). Des postes de gardes sont répartis à travers les deux aires d'interventions de l'ECWP pour limiter au maximum les activités de braconnage. Ces aires d'intervention sont composées de zones de réserves intégrales (30 595 km²) où la chasse est proscrite et de zones où la chasse est autorisée hors-période de reproduction (d'octobre à janvier sur 44 984 km²). Un suivi des populations est effectué tout au long de l'année dans les aires d'intervention, pour évaluer l'état et les tendances démographiques des populations et adapter au mieux les directives de conservation et translocation. Pendant la période de reproduction, des protocoles standardisés de point de comptage de mâles en parade et de suivi des nids sont mis en place pour estimer respectivement, les densités de mâles en parade et la productivité des femelles reproductrices. Hors période de reproduction, des points de comptages sont effectués sur les zones d'études pour estimer les densités d'oiseaux en automne et hiver. De 1996 à 2016, l'ECWP a lâché 2608 oiseaux équipés de radio-émetteurs et 1306 équipés d'émetteurs satellites et GSM. Ces suivis individuels ont notamment permis à Hardouin et al. (2014) de mettre en évidence un coût au lâcher sur la survie à court terme (3 mois) modulé par les conditions météorologiques et les périodes de lâcher (printemps ou automne). De plus, Hardouin et al. (2015a) ont observé une survie différentielle et dispersion asymétrique entre zones de réserve et zone de chasse, indépendantes des activités directes de chasse. Ces patrons de dispersion et de survie pourraient être expliqués par une hétérogénéité de la croissance locale et des densités indirectement causées par la pression de chasse et/ou l'hétérogénéité des habitats entre zones de réserve et de chasse (Hardouin et al. 2015a).

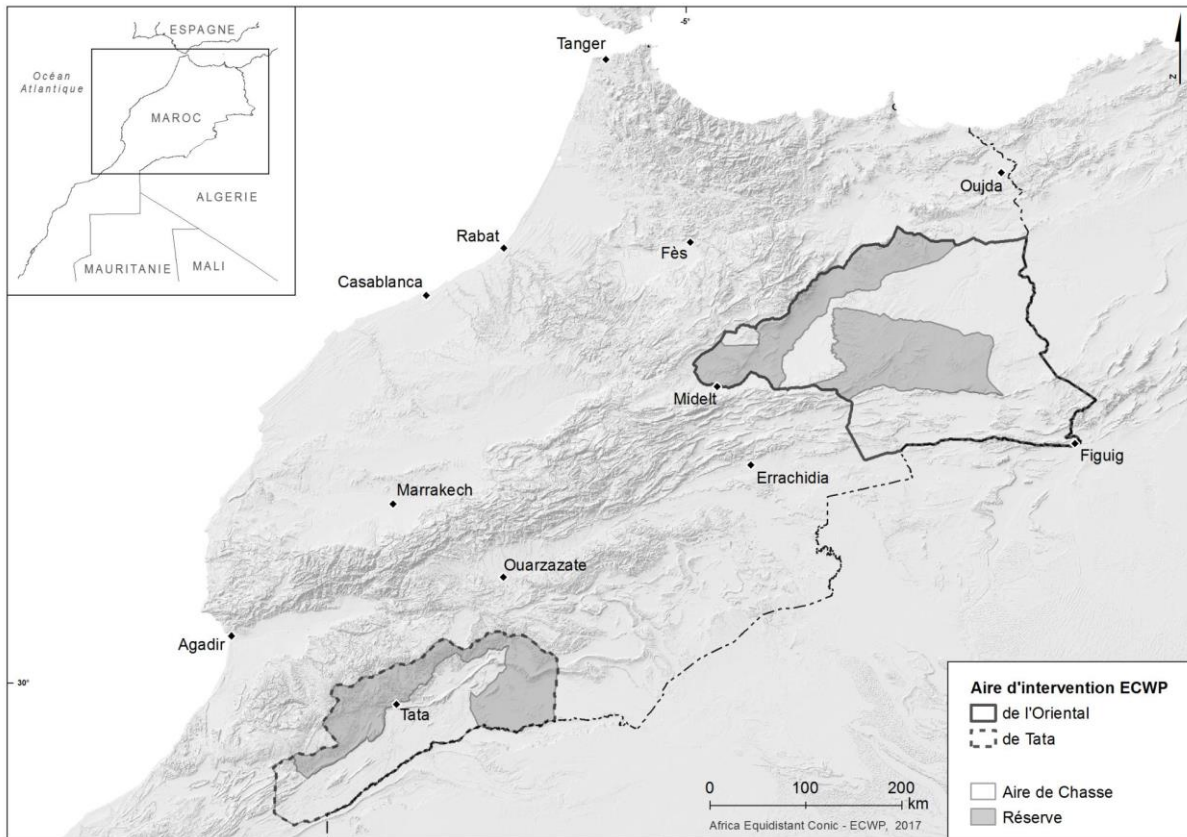


Figure 9. Localisation des aires d'intervention de l'ECWP au Maroc en 2017.

Depuis la création de l'ECWP, plusieurs campagnes de capture d'individus à l'état sauvage ont été effectuées (voir Hardouin et al. 2015b). Ces campagnes permettent d'identifier et marquer des individus nés à l'état sauvage. Ces données sont indispensables dans un programme de renforcement, car elles permettent de déceler la présence ou non de différences comportementales, biologiques et écologiques entre individus nés en captivité et individus nés à l'état sauvage. Les différentes études portant sur l'exploitation de l'espace écologique et des ressources trophiques n'ont pas mis en évidence de différences majeures entre individus lâchés nés en captivité et individus nés à l'état sauvage (Bourass & Hingrat 2015, Monnet et al. 2015a).

Introduction

Objectifs de la thèse

L'Emirates Center for Wildlife Propagation se caractérise par une volonté d'appliquer les standards et directives de l'IUCN concernant les translocations conservatoires (IUCN 2013), notamment à travers la mise en place de suivis longitudinaux de la population d'outarde Houbara en milieu naturel pour développer les connaissances sur l'espèce et adapter au mieux les stratégies de translocations. Les différents suivis ont permis d'acquérir un large savoir concernant le système de reproduction de l'outarde Houbara (Hingrat et al. 2005, 2007a), la sélection et l'exploitation de l'habitat par l'outarde Houbara (Hingrat et al. 2007a, 2008, Bourass et al. 2012b), sa distribution dans l'espace (Monnet et al. 2015b), la qualité de l'habitat des aires renforcées (Monnet et al. 2015b) ainsi que l'influence de différents facteurs environnementaux et stratégies conservatoires sur la survie et la dispersion des individus (Hardouin et al. 2012, 2014, 2015a, 2015b). Cependant il n'existe encore que peu d'études concernant les paramètres de reproduction dans la nature des outardes Houbara femelles et indices de productivité qui en découlent. Les seules études conduites dans ce domaine concernent l'outarde de Macqueen (Azar et al. 2017, Anderson & Deeming 2002, Combreau et al. 2002, Koshkin et al. 2016).

La productivité d'une femelle se définit par le nombre de poussins qu'elle amène à l'envol par saison de reproduction. Cette productivité peut s'estimer simplement en observant le nombre total de poussins à l'envol par femelle, ou de manière plus détaillée en mesurant chacun des paramètres de reproduction. Ainsi, la productivité d'une femelle est le fruit du nombre de nids initiés par saison de reproduction, du nombre d'œufs pondus par couvée et de sa capacité à amener les œufs à l'éclosion et les poussins à l'envol. Cette deuxième approche permet une compartimentation de l'évaluation des facteurs environnementaux et individuels influençant la productivité des femelles. Il est alors possible de mettre en évidence des réponses hétérogènes qui n'auraient pas pu être observées en se focalisant sur un indice unique de productivité. Un tel approfondissement dans l'étude des paramètres de reproduction chez l'outarde Houbara en milieu naturel n'a pour l'heure jamais été effectué. Cette évaluation précise des performances reproductrices des individus permet aussi de quantifier et comprendre l'influence de chaque paramètre de reproduction sur la productivité des femelles.

Les indices de productivité représentent avec les indices de survie, les principaux proxys des performances démographiques individuelles et sont donc des critères importants de

l'évaluation du succès de translocation. Ils permettent notamment de calculer un indice de fertilité (produit de la survie annuelle de la femelle, de sa productivité et du sex-ratio à la naissance) qui représente la capacité annuelle individuelle à produire des descendants (Caswell 2001).

L'étude des paramètres de reproduction permettra dans un premier temps d'approfondir les connaissances de l'écologie de l'outarde Houbara, d'obtenir de premiers indicateurs d'évaluation des stratégies de translocation et de compléter l'ensemble des paramètres démographiques mesurés par l'ECWP (survie, productivité, dispersion). Il sera alors possible de construire des modèles quantitatifs pour juger de la viabilité au long terme de la population renforcée d'outarde Houbara.

Cette thèse s'organise en 4 chapitres :

Dans le **premier chapitre**, nous étudierons les paramètres de reproduction des femelles lâchées en se basant sur les données de suivi des nids. Plus précisément nous regarderons comment les performances reproductrices varient en fonction de l'âge des individus et s'il existe des patrons de sénescence des performances reproductrices. Bien que largement étudiés en milieu naturel (Nussey et al. 2013), les patrons démographiques âge-dépendants (et en particulier la sénescence) ont rarement été identifiés chez des individus lâchés issus de programmes de translocation (voir Chantepie et al. 2016 pour une exception). Cette étude permettra d'examiner si des patrons âge-dépendants persistent chez les outardes Houbara femelles lâchées nées en captivité et cela malgré de potentiels coûts au lâcher. Il a été montré que les phénomènes de sénescence affectent le taux de croissance et la probabilité d'extinction de populations animales en milieu naturel (Robert et al. 2015b). Les résultats de cette étude pourraient donc nous permettre d'améliorer la précision de l'évaluation du succès du programme de renforcement.

Dans le **second chapitre**, nous chercherons à évaluer s'il existe un coût au lâcher sur les performances reproductrices des femelles lâchées en les comparant à celles de femelles nées à l'état sauvage. De nombreuses études ont déjà mis en évidence de plus faibles performances reproductrices chez les individus lâchés nés en captivité (Buner et al. 2011, Musil & Connelly 2009, Sarrazin et al. 1996). Cependant peu d'études se basent sur un suivi au long terme (voir Sarrazin et al. 1996, Bertolero et al. 2007 pour exceptions), permettant d'évaluer si ces différences persistent ou non malgré des phénomènes d'apprentissage et de sélection. Les

femelles étant toutes lâchées à un stade précoce de leur vie, il est particulièrement important de discriminer les effets de l'âge des effets « origine » (nées à l'état sauvage vs. lâchées).

Dans le **troisième chapitre**, nous nous intéresserons au lien entre performances reproductrices et habitat. La qualité de l'habitat réfère à la capacité de l'environnement à fournir les conditions appropriées pour la persistance des individus et d'une population (Hall et al. 1997). Sa caractérisation est donc un paramètre clé dans le succès d'un programme de translocation (e.g. caractérisation des zones préférentielles de lâcher, IUCN 2013, Seddon 2013). Dans ce cadre, des modèles de niches ont été utilisés pour développer un indice de qualité d'habitat (Monnet et al. 2015b), qui représente une probabilité de présence de l'espèce, en reliant des données d'occurrences spatiales à des paramètres environnementaux. Cependant, les conditions environnementales qui favorisent la présence d'une espèce peuvent différer des conditions qui favorisent ses performances démographiques (Kristan 2003). Les habitats qui favorisent la présence d'une espèce peuvent présenter de fortes densités locales exacerbant certains processus écologiques (compétition, prédation) néfastes sur les taux démographiques de l'espèce (Fernández-Bellon et al. 2016, Guisan & Thuiller 2005, Gunnarsson & Elmberg 2008, Oliver et al. 2012). De plus, ces processus écologiques peuvent être influencés par des dynamiques temporelles telles que la phénologie de l'espèce ou des événements stochastiques (Yang & Rudolf 2010). L'indice de qualité d'habitat développé par Monnet et al. (2015b) ayant vocation à être appliqué dans des actions de conservation, il est nécessaire d'en évaluer la capacité à prédire la qualité réelle de l'habitat. Nous chercherons donc à voir s'il existe un lien entre performances reproductrices des femelles et indice de qualité d'habitat et si ce lien est soumis à des dynamiques intra et interannuelles.

Enfin, dans le **quatrième chapitre**, nous nous appliquerons à mesurer l'influence des renforcements et de la chasse sur la viabilité de la population d'outarde Houbara. Le programme de renforcement de l'ECWP se trouve à l'interface entre objectifs conservatoires et exploitation des populations. Il vise à établir une population reproductrice stable, par l'intégration d'individus issus du programme de reproduction en captivité à la population reproductrice sauvage. A contrario, de nombreux programmes de renforcement avec des objectifs de chasses (e.g. prélèvement immédiat après lâcher, Sokos et al. 2008) ne prévoient et ne désirent pas l'intégration des individus lâchés dans la population reproductrice sauvage (Champagnon et al. 2012, 2013). Les connaissances acquises au cours de cette thèse et issues de travaux antérieurs nous permettront de développer des modèles quantitatifs de viabilité des populations (IUCN 2013) en prenant en compte la complexité et l'hétérogénéité inhérentes

Objectifs de la thèse

aux populations issues de translocations. Nous pourrons alors : (1) évaluer la dynamique de la population sous les conditions de renforcement et de chasse actuelles, (2) voir en quelle mesure l'effort de renforcement et la pression de chasse affectent la probabilité d'extinction de la population et (3) quantifier la contribution des individus reproducteurs lâchés à la dynamique et à la conservation de la population renforcée.

Méthodes : Le suivi des nids

Cette section présente le programme de suivi des nids d'outarde Houbara dans l'aire d'intervention de l'Oriental au Maroc, auquel j'ai pris part 4 années de suite (2013-2016) via la collecte et la saisie des données, la mise en place de nouveaux protocoles (suivi des nids avec pièges photographiques, identification des femelles aux nids avec outils de radio-identification) et la formation et la gestion des équipes de terrain.

Localisation des nids

L'étude des paramètres de reproduction des outardes Houbara femelles se fait principalement par le suivi et la collecte d'informations au nid. La localisation des nids est difficile, les femelles présentant un comportement cryptique. A cela s'ajoute l'étendue de l'aire d'intervention (Fig. 10) et des terrains de prospection hétérogènes et accidentés qui rendent les protocoles traditionnels de prospection (transects et points d'observation) difficilement applicables et peu rentables. Pour localiser les nids d'outarde Houbara, l'ECWP se base sur une collaboration avec les populations locales. Cette collaboration est fondée sur un système de prime pour chaque nid localisé. Ce système a historiquement été mis en place avec un double objectif : afin de réaliser les collectes d'œufs nécessaire à la création du stock reproducteur captif (Lesobre 2008) et comme mesure de protection et de sensibilisation au long terme pour limiter le braconnage des œufs. Au printemps, l'activité pastorale (élevages d'ovins et caprins) s'accroît avec l'arrivée des nomades qui se partagent les terres avec la population résidente. La steppe offre également d'autres ressources, comme les champignons, la truffe des sables ou « Terfez », notamment lors des années à fortes précipitations (El Enshasy et al. 2013). Pendant cette période, les membres de l'équipe écologie de l'ECWP et les gardes de l'aire d'intervention patrouillent à la rencontre des nomades et des cueilleurs de champignons pour obtenir informations et localisations des nids. Une fois qu'un nid est localisé, une position GPS est enregistrée. Une partie des nids est aussi localisée par le suivi des femelles équipées d'émetteurs VHF, GSM et PTT. Pendant la période de reproduction, les femelles équipées d'émetteurs VHF sont cherchées au moins une fois par semaine. Pour détecter des évènements de nidification chez les femelles équipées d'émetteurs GSM et PTT, les données de localisation sont examinées manuellement plusieurs fois par semaine.



Figure 10. Grande étendue steppique de l'Oriental marocain (Lieu-dit : Lethima) dans laquelle se retrouve l'outarde Houbara.

Une fois le nid localisé, les œufs sont individuellement marqués et mesurés (longueur, largeur et masse) par des membres de l'ECWP. La mesure des œufs permet en particulier de calculer un stade d'incubation des œufs et d'estimer leurs dates théoriques d'éclosion (voir « Supplementary materials » - Chapitre 1).

Visites des nids

Les nids sont visités de manière périodique, environ tous les 7 jours. A l'approche de la date théorique d'éclosion des œufs, la fréquence des visites augmente (tous les 2 à 3 jours). L'aire d'intervention étant étendue et très accidentée, l'accès aux nids s'effectue en véhicule tout terrain. Lors des visites, l'observateur agit et se comporte de façon à laisser le moins de traces possible de son passage. A chaque visite, différentes informations sont collectées telles que le nombre d'œufs, la présence ou non de poussins, l'observation ou non de la femelle, le comportement de la femelle, la présence d'empreintes d'outardes et de mammifères, la présence de coquilles d'œufs, de fientes, etc. Ces données permettent d'évaluer le statut du nid (actif ou non) et de déterminer s'il y a eu éclosion d'au moins un œuf ou non (Mabee 1997). Chez l'outarde Houbara, un nid est considéré en échec, si les œufs disparaissent entre deux visites sans aucune traces d'éclosions (e.g. traces d'éclosion : débris de coquilles,

empreintes/fientes de poussins, observation directe des poussins au nid, voir Mabee 1997) ou si les œufs ont été abandonnés (absence de la femelle ou d'indices présentant une activité au nid). Les visites périodiques et l'estimation du destin des nids (échec ou éclosion d'au moins un œuf) permettent par la suite de calculer le taux de survie journalier des nids (Encadré 1).

Encadré 1 : Taux de survie journalier des nids.

La survie d'un nid est définie comme la probabilité d'éclosion d'au moins un œuf (espèce avec poussins nidifuges) ou envol d'au moins un poussin (espèce avec poussins nidicoles). Dans le cadre du suivi de nid d'outarde Houbara, une survie apparente peut être estimée en faisant le ratio du nombre de nids où il y a eu éclosion d'au moins un œuf sur le nombre total de nids suivis. Cette survie apparente est biaisée positivement car les nids qui ont échoué pendant la phase de ponte et en début d'incubation sont sous-représentés (ils n'ont pas pu être localisés). De plus, les nids localisés tardivement ont une plus forte probabilité d'arriver à l'éclosion que des nids localisés à leur initiation (Mayfield 1961, 1975). Pour faire face à ces biais inhérents au calcul de survie des nids, Mayfield (1961, 1975) a développé une méthode de calcul de survie des nids prenant en compte le nombre de jours où le nid a été suivi (le temps d'exposition) et le nombre de nids suivis qui ont échoués. Cette méthode estime un taux de survie journalier des nids, la probabilité pour un nid avec au moins un œuf de survivre un jour. Le taux de survie journalier des nids de Mayfield se calcule de la façon suivante :

$$1 - \left(\frac{\text{Nombre de nids en échec}}{\text{Nombre total de jours d'exposition}} \right)$$

La méthode de Mayfield présente de nombreuses limites. Elle fait l'hypothèse que le taux de survie journalier des nids est constant dans le temps, ne permet pas d'évaluer des variations du taux de survie journalier en fonction de variables continues et demande à connaître les dates exactes d'échec et d'éclosion.

Depuis Mayfield (1961, 1975), de nouvelles méthodes ont été développées (Dinsmore et al. 2002, Shaffer 2004, Stephens 2003). Parmi les plus récentes, la méthode d'exposition logistique de Shaffer (2004) se base sur des modèles linéaires généralisés avec une probabilité de distribution binomiale et une fonction lien logit adhoc qui prend en compte le temps d'exposition entre deux visites. Elle permet de prendre en compte les variations du taux de survie journalier en fonction de variables continues (e.g. variables temporelles) et de facteurs. Elle ne nécessite pas de connaître la date exacte d'échec d'un nid, mais uniquement l'intervalle entre deux visites pendant lequel l'échec a eu lieu. Les taux de survie journaliers issus des modèles d'exposition logistique sont estimés par maximum de vraisemblance. La sélection des modèles peut donc se faire en se basant sur des approches de théorie de l'information utilisant des critères d'informations comme l'AICc (Burnham & Anderson 2002).

La méthode de Dinsmore et al. (2002) développée dans le logiciel MARK est similaire dans son approche statistique et produit des résultats semblables à celle de Shaffer (2004) (Rotella et al. 2004). Cependant l'approche de Shaffer (2004) offre une plus grande facilité et flexibilité dans la construction des modèles (e.g. mise en place d'interactions, inférence multi modèles) et permet de prendre en compte des effets aléatoires (Zuur et al. 2009).

Quel que soit la méthode utilisée, le calcul du taux de survie journalier permet par la suite d'obtenir une probabilité de survie des nids. Il suffit de ramener la valeur journalière au nombre de jours

considérés pour un nid qui atteint l'éclosion. Chez l'outarde Houbara, si l'on considère la phase d'initiation (4 jours en moyenne) et d'incubation (23 jours en moyenne) :

$$\text{Survie d'un nid} = \text{Taux de survie journalier}^{27}$$

Le principe de calcul du taux de survie journalier peut s'appliquer à d'autres suivis que le nid. Dans le cas d'espèces avec des poussins nidifuges, il est souvent difficile d'effectuer un suivi individuel des poussins et donc de calculer leur survie. La méthode de calcul de survie des nids permet de calculer une survie de la nichée. La nichée est une entité composée des poussins d'un même nid et la survie de la nichée est la probabilité qu'une femelle amène, depuis l'éclosion, au moins un poussin à l'envol. Dans le cas où la probabilité de recapture de la nichée est de 100% (e.g. femelles équipées d'émetteurs), on peut alors calculer un taux de survie journalier de la nichée : probabilité qu'une nichée avec au moins un poussin survive 1 jour (Matthews et al. 2012).

Suivi des nids avec pièges photographiques

Pour améliorer la précision du suivi des nids, un protocole de suivi avec pièges photographiques (PP) a été mis en place à partir de 2013 dans l'Oriental. L'utilisation de PP équipés de capteurs de mouvement et de changement de température et de flash infrarouge ont permis un suivi continu des nids de jour et de nuit (Encadré 2). Le déploiement de PP au niveau des nids vise à réduire l'effort de visite et à accumuler des données précises sur l'histoire de vie des nids tels que les dates exactes d'éclosion des œufs et d'échec, le nombre d'œufs éclos ou encore l'identification des espèces prédatrices des œufs d'outarde Houbara. Dans la mesure du possible, le PP est déployé le plus tôt possible suite à la découverte d'un nid pour obtenir l'histoire de vie la plus complète de celui-ci. Les PP sont placés au sol à une distance de 50 cm à 150 cm du nid selon la structure de l'habitat environnant (e.g. hauteur de la végétation, reliefs). Le PP est positionné de manière la plus discrète possible, attaché à un bosquet ou un caillou et dissimulé avec des filets de camouflages et débris végétaux environnant (Fig. 11). Ceci a pour but de réduire le dérangement auprès de la femelle et de minimiser la détection du PP par d'autres espèces (e.g. prédateurs, Herranz et al. 2002, Richardson et al. 2009). Les nids équipés de PP sont visités tous les 7 à 14 jours indépendamment de l'âge du nid. A chaque visite, l'état des batteries/piles et la capacité de la carte mémoire sont vérifiés. Le PP est récupéré uniquement quand le nid n'est plus actif : éclosion et départ des poussins du nid ou échec (disparition des œufs ou abandon). Un des principaux apports des PP a été l'identification de la guilda d'espèces prédatrices des œufs d'outardes au Maroc. Celle-ci est composée du renard roux (*Vulpes vulpes*), du chacal doré (*Canis aureus*), de chiens errants (*Canis lupus familiaris*), du hérisson du désert (*Paraechinus aetiopicus*), du grand corbeau (*Corvus corax*) et du corbeau brun (*Corvus ruficollis*) (Fig. 12). Les données de PP ont montré qu'au moins 74% des échecs sont causés

par des prédatons, le reste étant des abandons, destructions par piétinement de troupeaux et échecs par causes non identifiables. Sur les échecs identifiés comme prédatons, une grande majorité est le fait du renard roux (90%). Au total, entre 2013 et 2016, 122 PP ont été déployés sur 635 nids cumulant 8514 nuits de piégeage. Le suivi des nids avec des pièges photographiques n'est pas sans risque (Herranz et al. 2002). Leur présence peut occasionner des dérangements provoquant l'abandon du nid par la femelle, ou augmenter la détectabilité du nid par les prédateurs à cause des indices visuels et auditifs qu'ils produisent (Meek et al. 2014, Richardson et al. 2009). Dans notre cas, la présence de pièges photographiques n'a pas d'impact significatif sur le taux de survie journalier des nids suivis (Fig. 13, voir Annexe 1).



Figure 11. Pièges photographiques camouflés.



Figure 12. Prédation de nid d'outarde Houbara par A. un corbeau brun, B. un renard roux, C. un hérisson du désert et D. un chacal doré

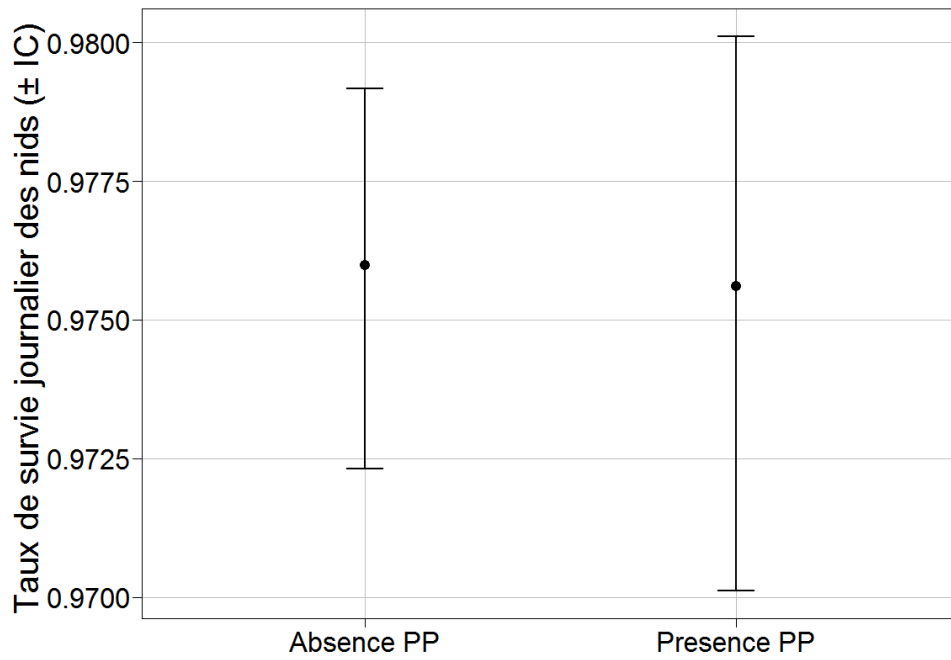


Figure 13. Taux de survie journalier des nids (± Intervalle de Confiance à 95%, IC) en fonction de la présence ou absence de piège photographique (PP) au nid.

Encadré 2 : Choix des pièges photographiques pour le suivi des nids et exploitation des données

On distingue au sein des pièges photographiques (PP) deux catégories. Les PP sans déclencheur automatique et les PP avec déclencheur automatique. Les PP sans déclencheur automatique prennent des photos à intervalle de temps régulier prédéfini. Ils présentent le désavantage de ne pas être sélectifs sur le déclenchement, consommant plus d'énergie et accumulant beaucoup de photos sans événements particuliers, dites « nulles ».

Les PP avec déclencheur automatique regroupent des PP avec déclenchement mécanique (e.g. l'animal déclenche le PP en marchant sur une dalle de pression) et les PP avec déclencheur infra-rouge. Les PP avec déclencheur infra-rouge peuvent être actifs ou passifs. Un PP avec déclencheur infrarouge actif produit un faisceau infrarouge depuis un émetteur vers un récepteur. Lorsque le faisceau est cassé par le passage d'un animal le PP se déclenche. Le déclencheur infrarouge passif consiste en plusieurs capteurs infrarouges (le nombre varie selon les modèles) qui « lisent » la température d'arrière-plan. Lorsqu'un animal passe devant ces capteurs, les mouvements et changements de températures produits par l'animal déclenchent la prise de photos (O'Connell et al. 2011).

Dans le cadre de notre suivi des nids, nous avons utilisés 7 modèles de PP à déclenchement infrarouge passifs et un modèle de PP sans déclenchement automatique. L'utilisation de différents modèles nous a permis d'en évaluer les performances et rentabilités, pour sélectionner par la suite ceux qui conviennent le plus au suivi des nids d'outarde Houbara. Le modèle sans déclenchement automatique a rapidement été exclu car il ne permet pas la sélection des événements permettant de définir le sort des nids (échec ou éclosion).

Les PP sont positionnés à même le sol pour en diminuer au maximum la détection. Ceci s'est avéré être un problème pour de nombreux modèles lors des déclenchements de nuit. Pour certains modèles, le flash infrarouge est trop puissant (et non réglable) et produit une surexposition de l'image (Fig. 14). Il est alors impossible d'identifier la cause du déclenchement (e.g. quelle espèce de prédateur). Les PP étant positionnés devant les nids, de simples mouvements de la femelle peuvent amener à une accumulation considérable de photos et consommer les batteries/piles en quelques jours. A l'opposé, certains PP ne se déclenchent pas car les fortes chaleurs empêchent les capteurs de distinguer les différences de températures entre l'arrière-plan et les objets en mouvement.



Figure 14. Comparaison des photos de nuits pour un piège photographique avec flash-infrarouge auto-ajustable (à gauche) et un piège photographique au flash trop puissant provoquant une surexposition de l'image (à droite).

Au final, trois modèles de PP ont été sélectionnés pour le suivi des nids (Moultrie M990i et Reconyx PC900 et HC600). Nous avons favorisé des PP avec des capteurs et des flashes infrarouges réglables ou auto-ajustables permettant d'obtenir des photos exploitables et consommant le moins d'énergie

possible. Par ailleurs, nous avons sélectionné des PP dont le flash infrarouge émettait à des longueurs d'ondes égales ou supérieures à 900 nm, pour réduire la détection des déclenchements de nuit par les mammifères (Meek et al. 2014). De nombreux PP ayant été perdus/volés/détruits (Fig. 15) lors de ces quatre années de suivi (n=20), le prix à l'unité a aussi été pris en compte dans la sélection finale.



Figure 15. PP retrouvé détruit (lentille brisée, écran et capteur infrarouge transpercés) lors de sa récupération sur un nid.

Le suivi continu des nids avec PP a engrangé la production d'une quantité considérable d'images (environ 1 500 gigaoctets en 4 ans). Un serveur dédié a été mis en place pour en permettre le stockage. L'exploitation des images pour estimer le sort des nids s'est fait au fur et à mesure des réceptions. L'analyse manuelle des images a été possible car elle s'est basée sur des questions précises : présence ou non de la femelle, présence ou non des œufs, présence ou non de poussins, présence ou non de prédateurs et d'évènement de prédation. Ces données permettront par la suite de répondre à d'autres questions : dynamique des abondances relatives des prédateurs, comportement de nidification des femelles, etc. (O'Connell et al. 2011, Ribic et al. 2012). Cependant, des outils de traitement automatique seront nécessaires pour en exploiter toutes les potentialités (Harris et al. 2010).

Identification des femelles lâchées aux nids

Les visites aux nids permettent de collecter des informations sur la femelle. Avant 2006, tous les oiseaux lâchés étaient marqués avec une bague aluminium à la patte gauche, présentant un code unique. Depuis 2006 les oiseaux ne sont plus bagués mais marqués avec une puce sous-cutanée encore appelée transpondeur (Fig. 16, TROVAN LID100 DorsetID, dimensions : 2.12 x 11.5 mm ; voir Hardouin et al. 2015b). Ce transpondeur est porteur d'un code alphanumérique unique qu'il est possible de lire en utilisant des outils de Radio Identification (RFID) dédiés. Enfin, depuis la création de l'ECWP, 3014 oiseaux équipés d'émetteurs ont été lâchés dans l'Oriental marocain (1937 avec des émetteurs VHF, 933 avec des émetteurs satellites et 144 avec des émetteurs GSM, voir Chapitre 2 pour les spécificités des émetteurs).



Figure 16. Transpondeur utilisé pour le marquage des outardes Houbara depuis 2006 (échelle supérieure de la règle en cm).

L'identification des femelles au nid s'est faite dans un premier temps par le suivi des femelles équipées d'émetteurs. Au total 167 femelles équipées d'émetteurs VHF ont été identifiées sur 332 nids, 48 femelles équipées d'émetteurs GSM ou satellite ont été identifiées sur 72 nids. Les femelles équipées d'émetteurs ont montré un taux de survie journalier des nids significativement plus faible que les femelles non-équipées d'émetteurs (Fig. 17, voir Annexe 1). Cette plus faible survie des nids pourrait être expliquée par de plus faibles conditions corporelles et physiologiques des individus équipés d'émetteurs (Barron et al. 2010).

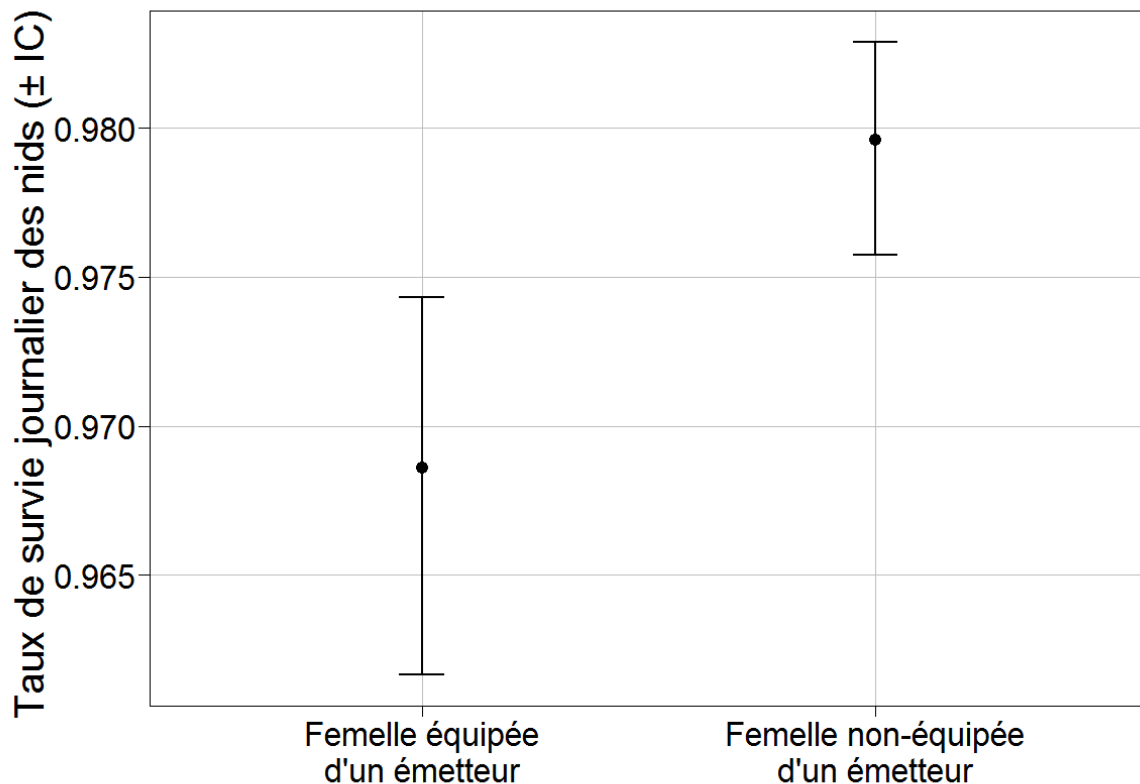


Figure 17. Taux de survie journalier des nids (\pm Intervalle de Confiance à 95%, IC) pour des femelles équipées ou non d'un émetteur.

Depuis 2013, un protocole d'identification des femelles lâchées non équipées d'émetteurs a été mis en place dans l'Oriental. Celui-ci se base sur le déploiement de lecteurs par RadioIdentification (RFID) sur les nids, permettant la lecture du transpondeur des oiseaux lâchés.

Identification des femelles lâchées avec les dispositifs de lecture RFID

Les systèmes de radio-identification (RFID) se composent du transpondeur (implanté dans l'oiseau) et d'un dispositif de lecture. Le transpondeur est enfermé hermétiquement dans une capsule de verre (Fig. 16). Il s'agit d'un dispositif passif qui nécessite une source d'énergie externe pour émettre l'information qu'il contient (code alpha-numérique). Le dispositif de lecture est constitué d'une antenne reliée à un boîtier décodeur branché à une batterie 12V (Figs. 18, 19). Dans le cadre de notre étude nous avons utilisé des antennes à armature carrée (25 x 25 cm) et octogonale (diamètre = 19 cm, Fig. 18). Celles-ci sont posées directement sur le nid (Fig. 20). Le choix des formes et formats a été défini par rapport aux dimensions des nids des outardes (diamètres des cuvettes) et retours de terrain. Lorsqu'une femelle pucée retourne sur son nid où se trouve l'antenne, le champ électromagnétique émis par l'antenne permet d'activer le transpondeur. Le transpondeur retourne alors un code signal vers l'antenne. Celui-ci est transféré au boîtier décodeur qui le traite et en extrait le code. Le dispositif de lecture déployé sur le nid est camouflé pour minimiser le dérangement et favoriser le retour de la femelle au nid. Les antennes sont recouvertes de sable et gravillons pour se confondre avec le substrat. Le décodeur et la batterie sont placés à distance du nid et couverts par des filets de camouflage, débris végétaux et cailloux pour se fondre dans l'habitat. L'ensemble est déployé pendant environ deux heures, pour laisser le temps à la femelle de retourner sur le nid et incuber les œufs. Un piège photographique est mis en place le temps du déploiement pour attester du retour ou non de la femelle. L'observateur peut, pendant le déploiement, se placer à distance du nid (700m-1000m) avec une longue vue. Ceci permet d'observer en temps réel le retour de la femelle et de retirer le dispositif plus rapidement. En début et fin de déploiement du dispositif, un transpondeur contrôle est passé au niveau de l'antenne pour attester de son bon fonctionnement. Au total 23 lecteurs placés sur 1222 nids ont permis l'identification de 580 femelles lâchées sur 657 nids. Dans 83% des cas, la femelle retourne au nid lorsque l'antenne est déployée. Le retour se fait en moyenne 35 minutes après le déploiement du dispositif et varie selon l'heure de la journée (Fig. 21). Lors de ces quatre années de suivis, le déploiement du dispositif a provoqué un seul abandon avéré de nid. La non-lecture du transpondeur, lorsque la femelle retourne sur le nid, peut signifier

que la femelle n'est pas pucée ou que le transpondeur n'a pas été lu (échec de lecture, encadré 3). La présence du lecteur RFID sur une courte période n'affecte pas significativement le taux de survie journalier des nids (Fig. 22, voir Annexe 1).



Figure 18. Phase de test des lecteurs avec antenne carrée et octogonale en captivité sur des outardes Houbara d'élevages.



Figure 19. Dispositif de lecture RFID déployé sur un nid.



Figure 20. Antenne octogonale du dispositif de lecture RFID sur un nid.

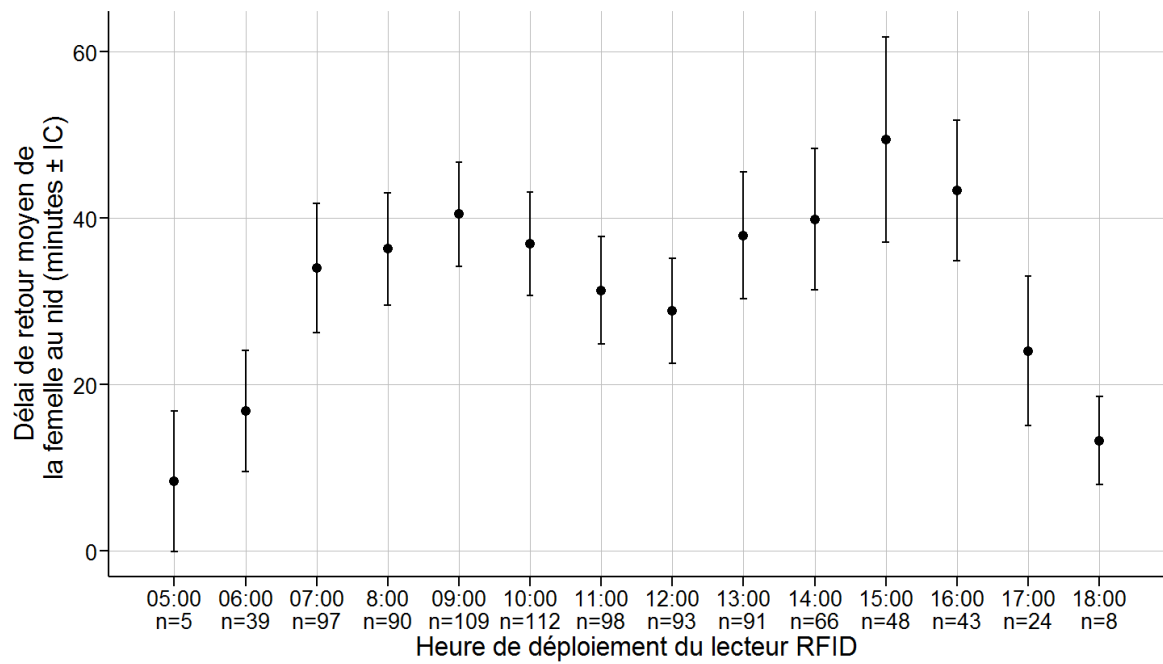


Figure 21. Délai de retour moyen des femelles au nid (en minutes \pm intervalle de confiance à 95%, IC) en fonction de l'heure de déploiement du lecteur RFID

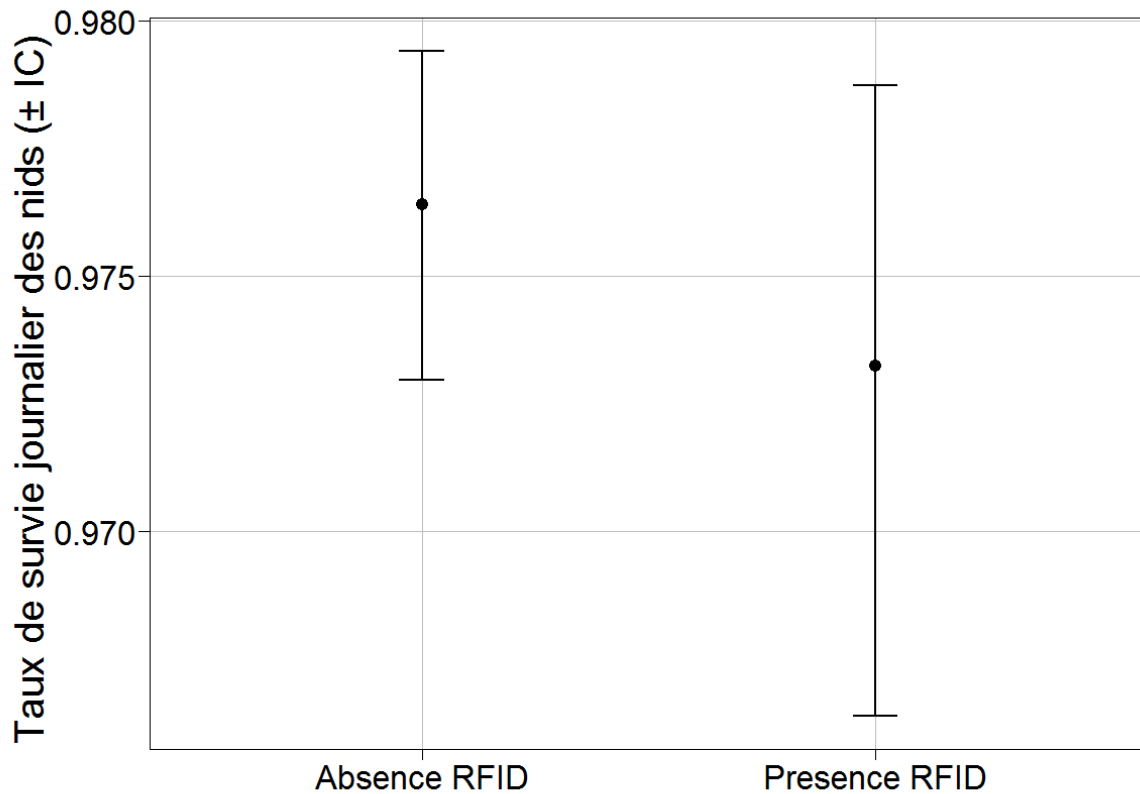


Figure 22. Taux de survie journalier des nids (\pm Intervalle de Confiance à 95%, IC) consécutif à la pose ou non d'un lecteur RFID sur le nid.

Encadré 3 : Echec de lecture des transpondeurs et développement des antennes

L'identification des femelles au nid a débuté avec le déploiement de lecteurs avec antennes carrées de 2013 à 2015. Pendant cette période, pour évaluer le taux de réussite des lecteurs avec antennes carrées, les lecteurs ont été déployés sur des nids de femelles lâchées équipées d'émetteurs (à l'identité connue). Pour ces nids, la non-lecture de puce définit donc un échec de lecture du transpondeur. Sur 20 nids, le taux d'échec de lecture a été de 30%. Le retour d'une femelle sur un nid équipé d'un lecteur RFID ne signifie donc pas que le transpondeur est lu si présent. Deux conditions font que le transpondeur peut ne pas être lu lorsqu'il est présent. La première est la distance entre le transpondeur et l'antenne qui émet le champ électromagnétique. Même si le constructeur précise une distance effective de 9-10cm, il s'avère que le transpondeur n'est pas toujours lu à cette distance. La seconde est l'orientation du transpondeur par rapport au champ électromagnétique émis par l'antenne (Benamara et al. 2016). La capacité d'activation optimale du transpondeur se fait lorsque le transpondeur est parallèle au champ électromagnétique émis par l'antenne : le champ électromagnétique traverse la bobine de cuivre du transpondeur de manière longitudinale, ce qui permet un transfert d'énergie sur toute la surface effective de la bobine de cuivre et l'activation du transpondeur (Benamara et al. 2016). Lorsque le transpondeur est perpendiculaire au champ électromagnétique : le passage du champ électromagnétique ne traverse pas toute la surface effective de la bobine de cuivre ce qui réduit le transfert d'énergie et rend plus difficile l'activation et la lecture du transpondeur (Fig. 23).

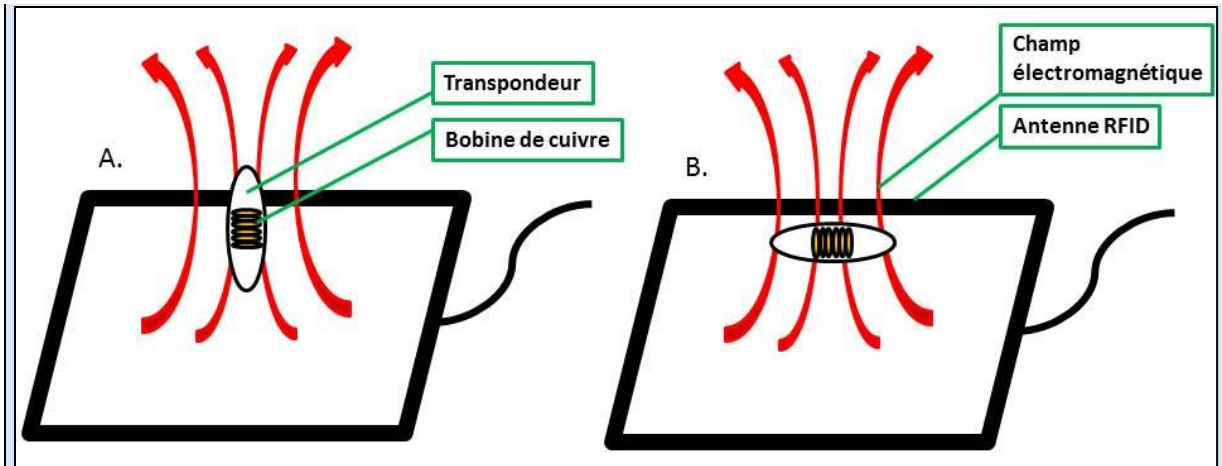


Figure 23. Orientation du transpondeur par rapport au champ électromagnétique (EM) émis par l'antenne. A. Orientation permettant le passage optimal du champ EM à travers la bobine de cuivre et activation du transpondeur. B. Orientation limitant le passage du champ EM à travers la bobine de cuivre et qui réduit le potentiel d'activation du transpondeur.

Face aux observations d'échecs de lecture nous avons développé des antennes plus petites, pour réduire la distance entre le champ électromagnétique et le transpondeur, et avec une armature octogonale pour augmenter le nombre d'angles d'émission des champs électromagnétique par rapport à la position du transpondeur. Ces antennes octogonales ont été déployées en 2015 et 2016. Le taux d'échec de lecture sur ces antennes est de 27%. La modification de la taille et structure de l'antenne n'a donc pas permis de réduire drastiquement le taux d'échec de lecture. Cela est peut-être dû au fait que les antennes octogonales, plus petites, émettent un champ électromagnétique moins puissant, réduisant la capacité d'activation du transpondeur malgré la réduction de la distance.

En 2015 lorsque les deux modèles sont déployés, les taux de retour aux nids sont proches : 85% pour les antennes octogonales et 82% pour les antennes carrés. En 2016, seules les modèles d'antennes octogonales ont été déployés sur les nids pour standardiser le protocole.

Capture des femelles aux nids

Des campagnes de captures de femelles aux nids ont été conduites en 1997-1998, 2001-2009 et 2015-2016. Ces campagnes visent à la capture de femelles nées à l'état sauvage pour les équiper d'émetteurs. Les femelles sont capturées en disposant des lacets en nylon autour des nids (Fig. 24, 25, voir Hardouin et al. 2015b). La capture d'une femelle au nid provoque l'abandon systématique du nid. Ainsi, avant la capture, les œufs sont collectés pour être intégrés au lot d'individus fondateurs du programme de reproduction en captivité. Des œufs en bois remplacent les œufs collectés pour assurer le retour de la femelle sur le nid. Une fois le dispositif de capture mis en place, les personnes en charge de la capture se placent à l'affût dans l'attente du retour et de la prise de la femelle dans les lacets. Au total 143 femelles nées à l'état sauvages et 40 femelles nées en captivité ont été capturées au nid.



Figure 24. Disposition des lignes de capture autour d'un nid. La femelle est retournée sur le nid sans se prendre dans les lacets.

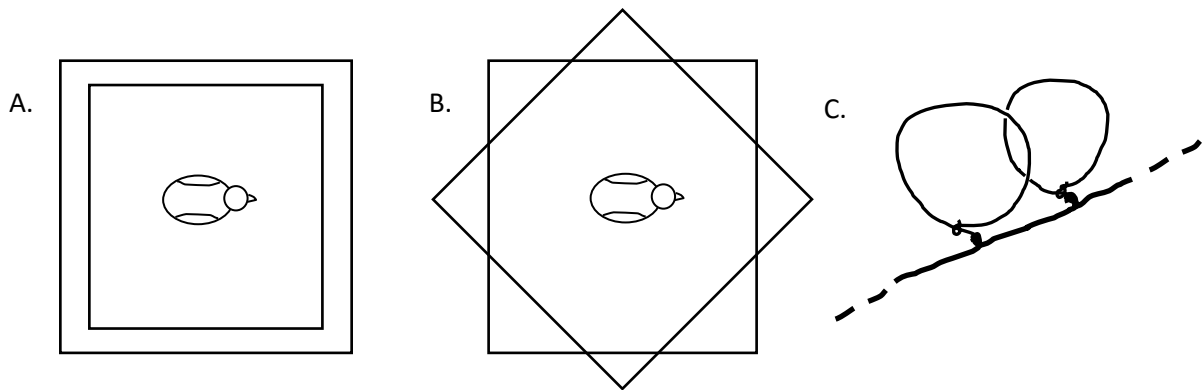


Figure 25. Disposition des lignes autour du nid, A. en carré, B. en étoile ; et C. disposition verticale des lacets.

Chapitre 1. Preuve de sénescence reproductrice chez les individus lâchés dans une population renforcée.

Résumé

Dans la nature, les variations des paramètres démographiques en fonction de l'âge, notamment les patrons de sénescence, ont des implications éco-évolutives majeures. Malgré l'accroissement du nombre d'études sur la sénescence en nature, ces patrons qui sont cruciaux pour l'évaluation de la dynamique de populations, telles que les populations issues de translocation, restent encore peu explorés. En nous basant sur 15 années de suivi de nids d'une population renforcée d'outarde Houbara nord-africaine, nous nous sommes intéressés aux variations des performances reproductrices de femelles lâchées produites en captivité en fonction de leur âge. Nous avons identifié 781 femelles, âgées de 1 à 10 ans, sur 1094 nids (Fig. 26). Nous avons ensuite examiné comment l'âge des femelles influence la date d'initiation des nids, la taille de la couvée, le volume des œufs, le taux de survie journalier des nids et des nichées ainsi que l'évolution de ces patrons âge dépendant en fonction de différentes conditions environnementales. La plupart des paramètres de reproduction montraient des variations, suggérant une augmentation des performances reproductrices avec l'âge chez les jeunes individus (de 1 à 3 ans). Chez les individus les plus âgés (> 7–8 ans) la taille de la couvée et le volume des œufs diminuent avec l'âge, en concordance avec les théories de la sénescence et de précédents résultats obtenus en captivité sur l'outarde Houbara nord-africaine. Finalement, nos analyses ont dévoilé une interaction significative entre l'âge des femelles et le niveau de précipitation précédant la saison de reproduction sur la taille de la couvée. Cette interaction suggère des capacités différentielles des femelles à augmenter leur investissement reproducteur en fonction de leur âge. Notre étude suggère que l'histoire de vie des individus lâchés produits en captivité n'est pas affectée par les protocoles de translocation et fournit des directives pour la prise en compte de patrons âge dépendants dans des modèles de viabilité des populations.

Mots-clés : Age, outarde Houbara, reproduction, translocation

Chapitre 1. Preuve de sénescence reproductrice chez les individus lâchés dans une population renforcée.

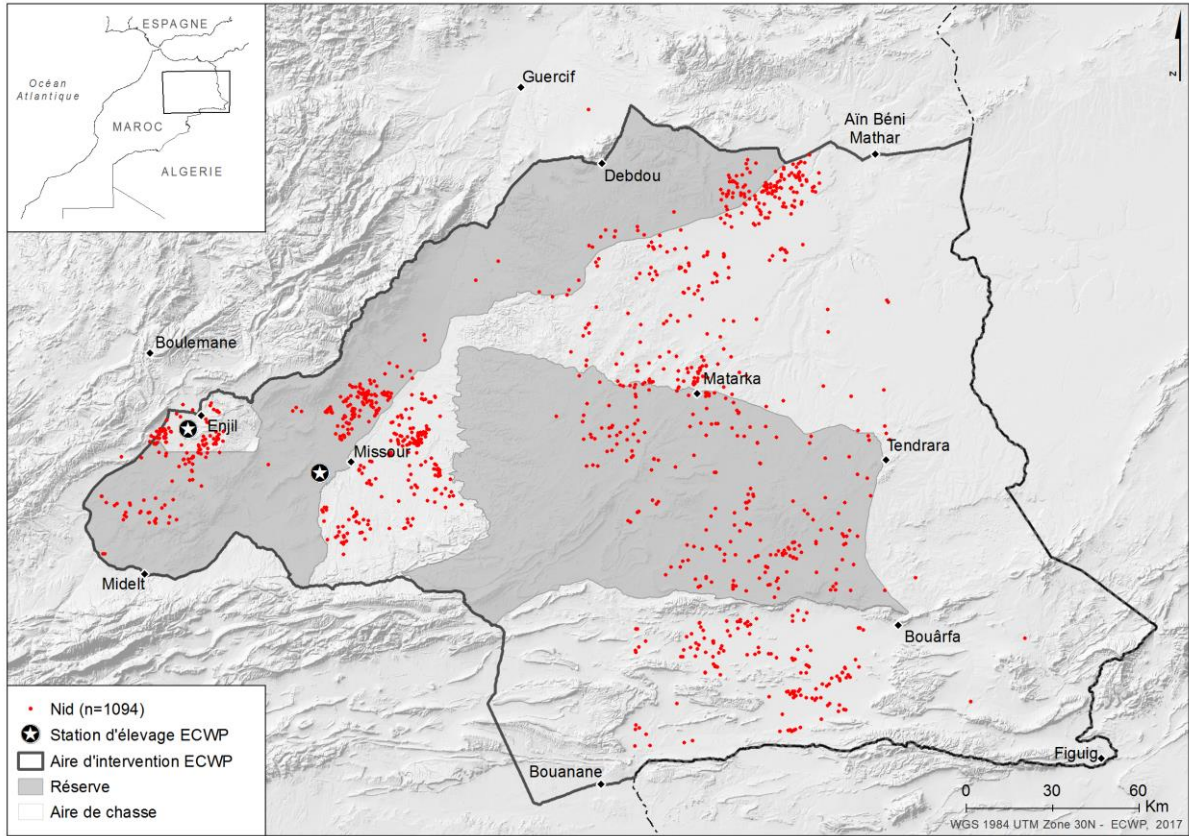


Figure 26. Distribution de 1094 nids de femelles lâchées recensés entre 2002 et 2016 dans l'aire d'intervention ECWP de l'Oriental marocain.

Article 1. Evidence of reproductive senescence of released individuals in a reinforced bird population

Bacon Léo, Hingrat Yves, Robert Alexandre

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Chapitre 1. Preuve de sénescence reproductrice chez les individus lâchés dans une population renforcée.



Evidence of reproductive senescence of released individuals in a reinforced bird population



Léo Bacon^{a,b,*}, Yves Hingrat^{a,c}, Alexandre Robert^b

^a Emirates Center for Wildlife Propagation, PO Box 47, 33250 Missour, Morocco

^b Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Museum National d'Histoire Naturelle, CP 135, 43 rue Buffon, 75005 Paris, France

^c RENEKO International Wildlife Consultants LLC, PO Box 61741, Abu Dhabi, United Arab Emirates

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ABSTRACT

In free-ranging populations, age-dependent variation in fitness related parameters, in particular the pattern of senescence, has major eco-evolutionary implications and potential influence on population dynamics. Despite the recent surge of studies of senescence in the wild, senescence patterns in species for which population dynamics assessments are crucial, such as translocated populations, remain virtually unexplored. Based on a 15-year nest survey of a North-African Houbara bustard population in Morocco, we investigated age variation in the breeding performance of captive-bred females released in the wild. We identified 781 females, from 1 to 10 years of age, on 1094 nests. We examined how age influenced nest initiation date, clutch size, egg volume, daily nest survival and daily brood survival, as well as whether age-dependent patterns varied according to environmental conditions. Most breeding parameters exhibited variation, suggesting an increase in breeding performance with age in young females (those from 1 to 3 years old). In older females (> 7–8 years old), the egg volume and clutch size decreased with age, in concordance with expectations from senescence theories and previous empirical results obtained from captive Houbara bustards. Finally, our analysis uncovered a significant interaction between age and the amount of precipitation prior to the breeding season on clutch size, suggesting differential abilities of females of different ages to increase their breeding investment. Our study suggests that life histories in translocated individuals are not affected by translocation protocols and provides insights for implementing age dependencies in population viability assessments.

1. Introduction

In wild animals, variation in fitness-related parameters with age has major eco-evolutionary implications (Charmantier et al., 2006) and a potentially strong influence on population dynamics and viability (Robert et al., 2015a; Chantepie et al., 2016). Although age-demography relationships can exhibit a diversity of patterns (Jones et al., 2014), most studies of vertebrates, both in captivity and in the wild, describe a characteristic bell-shaped trend of fitness related parameters divided into youth, adulthood and senescent stages (Lynch et al., 2010; Oro et al., 2014). The increase in performance in early ages can be explained (non-exclusively) by the selection of good quality individuals (the selection hypothesis, Lescroël et al., 2009), by the increase in experience or physiology (the constraint hypothesis, Curio, 1983) and the adaptive restraining of reproductive effort by young individuals (the restraint hypothesis, Curio, 1983). For ageing individuals, a decrease in demographic parameters is expected; this process is referred to as senescence. Senescence is caused by internal physiological degeneration

(Kirkwood and Austad, 2000) occurring in relation to the decrease of the force of selection with age (Charlesworth, 1994). In the field of evolutionary ecology, it has been argued for decades that animals in the wild fail to senesce due to high extrinsic mortality probability (Medawar, 1952; Kirkwood and Austad, 2000, discussion in Nussey et al., 2013). However, in recent years, new evidence enabled by longitudinal individual-based population surveys has clearly demonstrated that senescence commonly occurs in free-ranging populations (Nussey et al., 2008, 2013).

In addition to age variation, wild populations exhibit temporal and spatial variation in demographic parameters due to external factors (Parmesan, 2006), and the link between individual age and breeding performance or survival may be condition dependent (Reichert et al., 2010). It has been suggested that the effects of environmental conditions will be stronger on age classes with poor intrinsic abilities and conditions (Bunce et al., 2005; Pardo et al., 2013), so that differences in demographic parameters between ages will be greater in stressful environments (Bunce et al., 2005; Nussey et al., 2008). In contrast, if low-

* Corresponding author at: Emirates Center for Wildlife Propagation, PO Box 47, 33250 Missour, Morocco.
E-mail address: bacon.leo@gmail.com (L. Bacon).

quality individuals temper their reproductive investment to reduce costs when conditions are poor (Cubaynes et al., 2011; Robert et al., 2012), one may expect that differences in average reproduction performance between age classes will be greater in favourable environments (discussion in Oro et al., 2014; Robert et al., 2015b).

Conservation translocations are increasingly used to manage threatened species and to maintain or establish viable populations in the long term (Armstrong and Seddon, 2008). Translocated populations are likely to suffer demographic costs in terms of survival (Hardouin et al., 2014) and reproduction (Sarrazin et al., 1996), especially in translocations relying on captive breeding (Robert, 2009). Thorough assessments of these demographic costs and of their potential effects on the life history of released individuals are nevertheless rarely done, because they require high quality demographic data, which are generally lacking due to insufficient monitoring effort (Bertolero et al., 2007). Although now commonly documented in the wild in many taxa (Nussey et al., 2013), the effects of potential translocation costs on realized senescence patterns remain virtually unexplored (but see Chantepie et al., 2016 for a recent exception concerning actuarial senescence).

Here, we argue that the documentation of senescence patterns in translocated populations is of strong importance for (1) assessing whether translocated individuals senesce in the wild despite potential demographic translocation costs or phenotypic changes; and (2) improving the reliability of long-term assessments of the success of individual translocation programmes. We aim to investigate how breeding performance varies according to the age of released captive-bred individuals in a reinforced bird population and whether such age-related patterns vary according to environmental conditions. We used data collected from a longitudinal nest survey of the North-African Houbara bustard (*Chlamydotis undulata undulata*, hereafter Houbara) in eastern Morocco completed between 2002 and 2016. Previous studies on captive populations of Houbara have shown strong senescence trends in female breeding parameters (Chantepie et al., 2015; Preston et al., 2015) affecting egg productivity and chick mass at hatching. However, those results were obtained from captive populations subject to controlled environmental conditions (food and water ad libitum). Further investigation is needed to corroborate if similar age patterns occur in captive-bred females released in the wild. Since populations in the wild are exposed to higher levels of environmental stressors, one can expect mitigated age-dependent patterns and variation in breeding parameters as functions of environmental conditions. The Houbara is found in semi-desert habitats where meteorological conditions are highly variable between years and where water is a primary limiting factor (Gamoun, 2016). Under such environmental conditions, variation in temperature and precipitation may have major consequences on food resource availability, ecological processes (Brown et al., 1997; Gamoun, 2016), and breeding performance in bird species (Morales et al., 2002; van Heezik et al., 2002; McCreedy and van Riper, 2014).

We focused on five breeding parameters: nest initiation date, clutch size, egg volume, daily nest survival, and brood survival. Senescence in breeding parameters is expected to be primarily caused by physiological degradation (Angelier et al., 2006). Egg production (size and number) is known to be highly influenced by physiological conditions (Williams, 2001; Christians, 2002). Conversely, laying date as well as nest and brood survival are highly influenced by external factors (e.g., meteorological conditions, nest predators) and can be positively influenced by female competence, which is expected to increase with age (see discussions in Wooller et al., 1990 and Pärt, 1995, 2001). Therefore, we expected that clutch size and egg volume would experience particularly strong reductions in older individuals. In contrast, since female competence is expected to increase sharply with age in young females, we expected strong reductions in the precocity of nest initiation, nest survival, and brood survival in the youngest females.

Based on previous studies of birds in captive conditions and knowledge of the species' biology, we hypothesized three functional age

classes (see Chantepie et al., 2015, 2016): youth, adulthood and senescent ages, and made the following predictions:

1. Breeding performance will be lower in young birds (i.e., age < 2-years based on knowledge of the distribution of recruitment age, Preston et al., 2015) and in senescent individuals compared to adults, with more marked reduction in the precocity of nest initiation, nest survival and brood survival in younger females and more marked reduction in clutch size and egg volume in senescent individuals.
2. Meteorological conditions (temperature and precipitation) prior to the breeding season will constrain the breeding performance of all individuals. However, young, adult, and senescent individuals will respond differently to varied meteorological conditions.

2. Methods

2.1. Biological model and study area

The Houbara is a medium-sized bustard inhabiting semi-desert steppes from North Mauritania to Egypt. It is a ground-nesting, gyne-parental incubating species breeding from mid-February to mid-June. Females generally lay two or three eggs, at 2.5-day intervals, which they incubate on average for 23 days (Gaucher, 1995). Houbara chicks are nidifugous but rely on the dams to be fed for the first ten days after hatching and fledge at a mean age of 60 days (Saint Jalme and van Heezik, 1996; Hardouin et al., 2012).

Over the last few decades, the Houbara population has greatly declined throughout the species' range due to habitat degradation, poaching and over-hunting (Lacroix et al., 2003; Saint Jalme and van Heezik, 1996). This population decline led to the creation, in 1995, of the Emirates Center for Wildlife Propagation (ECWP) based in eastern Morocco (Lacroix et al., 2003). The ECWP captive breeding programme aims to increase the population size of the threatened Houbara throughout its range via regular releases of captive-bred individuals.

The present study was conducted in eastern Morocco (see Fig. A, Supplementary Appendix A). The study area encompasses an area of 50,000 km² and is characterized by an arid climate marked by irregular rainfall and cold winters. Hunting is allowed from October to January and is delimited to specific hunting areas totalling 64% of the managed area.

2.2. Release and tagging procedure

From 1996 to 2016, 108,486 birds were released in North Africa (94,374 in the study area). Within the study area, the overall number of birds released progressively increased over the years (from 28 in 1996 to 9084 in 2016), with an increase in the number of release sites and a decrease in the group size per release (Hardouin et al., 2014). The numbers of birds in release groups varied between sites (from 4 to 498, median = 18). Houbara were released at an average age of 8 ± 3 (standard deviation) months in spring (from March to May), autumn (from September to November) and, since 2003, at an average of 3 ± 0.6 months of age in summer (June). Autumn releases were conducted in non-hunting areas to avoid direct mortality and disturbance due to hunting. Over the study period, all released Houbara were individually marked with either aluminium rings (1996–2005) or electronic transponders (2006–2016). A total of 3014 individuals were also equipped with transmitters (see Supplementary Appendix B and Hardouin et al., 2015).

2.3. Data collection

2.3.1. Breeding parameters

Five breeding parameters were assessed from survey data collected from 2002 to 2016 (the number of years of survey data varied among

breeding parameters; this is mentioned below in cases where some survey years are missing).

2.3.1.1. Nest survey and nesting female identification. Nests were located through a collaborative survey with local shepherds and from individually tracked females. Nesting females were then identified based on ad hoc Radio Frequency Identification (RFID) technologies or their fitted transmitters (see details on identification techniques and sample sizes in supplementary Appendices B and C, respectively). Overall, we identified 781 captive-bred females from 1094 nests between 2002 and 2016 (see Supplementary Appendix C). The age of each female was estimated from its birth date in captivity and ranged from 1 to 10 years. Nest monitoring effort was constant between years (see Supplementary Appendix D). Visits occurred on average every 5 ± 3.31 days. In addition, since 2013, camera traps were deployed on some of the monitored nests ($n = 387$, see Supplementary Appendix E), providing a continuous survey effort and more accurate assessments of nest fate. Nests equipped with camera traps were visited on average every 8 ± 4.17 days. Nest failure was considered for a visit interval if the clutch disappeared without signs of hatching (Mabee, 1997) or was abandoned. We considered a nest to have survived if at least one egg hatched (Mayfield, 1975).

The clutch size was defined as the maximum number of eggs observed in the nest. Since 2003, the length, width (to the nearest hundredth cm), and mass (to the nearest tenth of a gram) of each egg were measured. The width and length of eggs were then used to calculate the egg volume (Vol) in cm^3 (see Supplementary Appendix F). The nest initiation date was estimated from the calculation of the eggs' incubation stage (in days) at the time of measurement (see Supplementary Appendix F). Sample size differences between breeding parameters are detailed in Supplementary Appendix G.

2.3.1.2. Brood survey. Assessing breeding success after hatching and before fledging in species with nidifugous chicks is challenging. It requires the marking and close monitoring of all individuals, a delicate operation that may affect chick survival at this very sensitive stage of life (Barron et al., 2010). As such, we chose not to mark chicks but rather assessed the fates of broods through the monitoring of brooding females. Therefore, between 2002 and 2014, nesting females fitted with VHF transmitters that brought at least one egg to hatching were evaluated at least once a week. Brood failure was considered for a female monitoring interval if the entire brood disappeared before 60 days of age (Combreau et al., 2002; Hardouin et al., 2012). In total, we monitored 152 broods from 107 captive-bred females fitted with VHF transmitters. The ages of the females monitored with a brood ranged from 1 to 8 years (see Supplementary Appendix C).

2.3.2. Statistical analyses

2.3.2.1. Nest and brood survival analyses. We used the logistic exposure approach of Shaffer (2004) to estimate the daily nest survival rate (probability of a living nest to not fail in one day; see details in Supplementary Appendix H). As recommended by Grant and Shaffer, 2012, we included the nest age (calculated from nest initiation dates) as a covariate in the daily nest survival analysis. Therefore, nests with unknown initiation dates were excluded from the analysis (see Appendix G for sample sizes).

The same statistical approach was used to study brood survival, with the exception that the exposure period started at hatching and ended at 60 days for successful broods (Combreau et al., 2002, Hardouin et al., 2012, see details in Appendix H).

2.3.2.2. Clutch size, egg volume and initiation date. The clutch size was analysed based on ordinal regression using cumulative linked mixed models (CLMMs, Christensen, 2015). Egg volume and initiation dates were analysed using linear mixed models (LMMs) fitted by maximum likelihood with a Gaussian distribution and an identity link function.

2.3.2.3. Covariates. For each breeding parameter, we evaluated the effects of the age of the female (FAge, in years) and the quadratic effect of the age (FAge²). Additionally, we used several temporal and environmental covariates in our models, the number of which depended on the response variable (details in Supplementary Appendix I). For each nest, we extracted from the Global Land Data Assimilation System (GLDAS v001 monthly data, Rodell et al., 2004), the average surface temperature (Temp, in °C), and precipitation (Prec, in mm/24 h) in the study area during the winter (December to February) preceding the breeding season (see Fig. J.1 and J.2 Supplementary Appendix J) as potential indicators of inter-annual variation in subsequent breeding performance based on previous studies of bustard species (Morales et al., 2002; van Heezik et al., 2002) and other birds inhabiting arid environments (McCreech and van Riper, 2014). To account for the variation in breeding performance within the breeding season, we included the nest initiation date (or hatching date for the brood survival) in Julian days (Date). If the nest initiation date was not available, we used the date of the first nest visit, as both dates were highly correlated (Pearson $r > 0.9$). Finally, we considered temporal variation of the daily survival rate of the nest and brood by including their ages (Nage and Bage, in days) and their quadratic effects (Nage² and Bage²).

2.3.2.4. Multi-model inference. For the analyses, all covariates were rescaled: centralized and standardized by two times the standard deviation (Gelman, 2008).

We first examined the relationship between breeding parameters and covariates by developing sets of candidate models that included all combinations of the related additive effects without female age \times covariate interactions. As a second step, we specifically investigated whether the relationships between breeding performance and the covariates varied as functions of the age of the female. We achieved this by developing a set of candidate models that included additive effects, quadratic effects (FAge² for all breeding parameters and Nage²/Bage² only for daily survival rates) and first-order interactions between the age of the female and the other covariates. We partitioned our analysis into two separate steps (additive effects only and additive plus quadratic and interaction effects) because we were interested in assessing main (additive) effects and because the use of model-averaging techniques (see below) to assess additive effects is irrelevant when quadratic and interaction effects are present (Banner and Higgs, 2017).

Many convergence failures occurred when including meteorological effects and analysing interaction effects for daily brood survival rates. Therefore, we only investigated quadratic effects of female age and brood age, excluding meteorological covariates and interactions from the global models.

The year, female identity, and nest identity nested within female identity (only for egg volume analyses) were incorporated as random effects in all models.

We ranked models using the Akaike Information Criterion corrected for small sample sizes (AICc). We estimated robust model-averaged coefficients (β) from the set of best models ($\Delta\text{AICc} < 2$; Burnham and Anderson, 2002) for each step of the multimodel inference, based on their AICc weights (the relative likelihood of candidate models based on their ΔAICc). We assumed significance of β for the covariates if their 95% unconditional confidence intervals (95% CIs) did not include zero.

2.3.2.5. Predictions as functions of the age of the female. If significant averaged coefficients of the female age covariates or interactions were observed from the candidate models, we graphically represented the focal breeding parameters as functions of the female age using Generalized Additive Mixed Model predictions (GAMM, Wood, 2006) with cubic regression splines and the number of knots equal to the number of age classes (Simon Wood, personal communication). The same random effects were applied as for the multimodel inference.

Because ordinal regressions with random effects are not implemented in GAMMs yet, we predicted the clutch size as a function of the female's age using GAMM assuming a Gaussian distribution (see Supplementary Appendix K).

2.3.2.6. The age of the female–nest initiation date relationship. Many studies have shown that nest initiation date is influenced by the age and/or experience of the breeding individuals, explaining the variation of breeding performances during the breeding season (e.g., Christians et al., 2001). In our models, considering the nest initiation date may explain a large proportion of the variance in breeding parameters (Bacon et al., 2017). To examine if age effects were mediated by nest initiation dates, we performed additional analyses of breeding parameters without including the nest initiation date covariate in the global models. We used the same multi-modelling approach in two steps as explained above.

All analyses were conducted using R 3.2.4 (R Development Core Team, 2016) and the packages lme4 1.1.7 (Bates et al., 2015), Ordinal 2015.6–28 (Christensen, 2015), MuMIn 1.13.4 (Barton, 2015), nest-survival (Herzog, 2009) and gamm4 0.2–3 (Wood and Scheipl, 2015).

3. Results

Overall, nest initiation dates ranged from March 10th to May 4th (first and ninth deciles), with an average nest initiation date of April 6th. Clutches were mainly composed of 2 (47%) or 3 (48%) eggs. Clutches of 1 (4%) and 4 eggs (<1%) were much less common. The average clutch size was 2.44 eggs (95% confidence interval [2.41, 2.48]), with a mean egg volume of 61.88 cm³ [61.65, 62.11]. The average daily nest survival rate and daily brood survival rate were 0.972 [0.969, 0.975] and 0.977 [0.972, 0.982], respectively.

We analysed the effects of dependent covariates on five breeding parameters based on a common statistical approach. To clarify the results, we summarize the effects of each covariate on various breeding parameters in separate paragraphs.

From the AICc ranking and model averaging, the first set of candidate models (i.e., additive effects) revealed significant negative effects of the initiation date on the daily nest survival rate, clutch size, and egg volume (Table 1).

The daily nest survival rate significantly decreased with the age of the nest, while the daily brood survival rate increased with the age of the brood (Table 1; see Fig. L Supplementary Appendix L).

The analysis also revealed significant positive effects of precipitation on the daily nest survival rate (Table 1).

Finally, as their age increased females laid clutches earlier in the season, produced larger eggs, and achieved higher brood survival (Table 1).

The second set of candidate models (step 2: quadratic effects and interactions, Table 1) revealed significant quadratic effects of the female age on nest initiation date, egg size, and clutch size. We also observed a strong negative interaction of the age of the female and precipitation on clutch size.

For clutch size and egg volume, GAMMs revealed non-monotonic variation of breeding parameters with the female age, consistent with the occurrence of maximal reproductive performance at intermediate ages (Fig 1A and B). One-year old females laid small clutches comprised of small eggs. Their performance increased at intermediate ages. After 8 years of age, this trend was consistently reversed.

For brood survival and nest initiation date, an increase in performance was observed for young females, followed by stabilization for older individuals (Fig 1C and D).

GAMM predictions of the interaction effect Fage × Prec on clutch size showed that precipitation had no effect on clutch size in young females. However, from the age of 3, females significantly increased their clutch size with high amounts of precipitation. The results further indicated that the senescence pattern occurred independently of

Table 1

Model-averaged coefficients (± 95% CIs) of covariates from the two sets of best models for all breeding parameters. 1. The first analysis focuses on the additive effects of the covariates. 2. The second analysis includes additive, quadratic and interaction effects.

Covariates	DNSR	DBSR	Clutch size	Egg volume	Date
1. Additive effects (first set of candidate models)					
FAge	0.17 [− 0.06, 0.39]	0.85 [0.17 , 1.52]	0.19 [− 0.10, 0.47]	1.45 [0.80 , 2.10]	− 5.19 [− 8.10, − 2.28]
Prec	0.30 [0.05 , 0.55]	−	0.19 [− 0.46, 0.83]	− 0.13 [− 0.76, 0.49]	− 2.55 [− 8.35, 3.25]
Temp	− 0.10 [− 0.35, 0.15]	−	− 0.22 [− 0.95, 0.52]	0.12 [− 0.54, 0.78]	− 4.47 [− 10.74, 1.81]
Nage	− 0.98 [− 1.22, − 0.75]	−	−	−	−
Bage	−	0.72 [0.11 , 1.34]	−	−	−
Date	− 0.23 [− 0.45, − 0.02]	− 0.07 [− 0.52, 0.39]	− 1.20 [− 1.50, − 0.90]	− 1.97 [− 2.47, − 1.48]	−
2. Additive, quadratic and interactions effects (second set of candidate models)					
FAge ²	− 0.04 [− 0.42, 0.34]	− 0.75 [− 1.56, 0.05]	− 0.74 [− 1.21, − 0.27]	− 2.47 [− 3.38, − 1.55]	7.48 [2.81 , 12.15]
Nage ²	− 0.11 [− 0.49, 0.26]	−	−	−	−
Bage ²	−	− 0.49 [− 1.65, 0.66]	−	−	−
FAge*Prec	− 0.15 [− 0.96, 0.66]	−	0.80 [0.24 , 1.36]	not selected	not selected
FAge*Temp	− 0.41 [− 0.93, 0.12]	−	not selected	not selected	not selected
FAge*Nage	− 0.19 [− 0.68, 0.29]	−	−	−	−
FAge*Date	0.23 [− 0.17, 0.64]	−	0.40 [− 0.09, 0.90]	0.16 [− 0.69, 1.01]	−

Averaged coefficients of additive effects are not presented in analysis 2 because the use of model-averaging techniques to assess additive effects is irrelevant when quadratic and interaction effects are presents. Coefficients are in bold, where 95% CIs do not include zero. “Not selected” indicates that the covariate was not selected in the best set of models, and “−” indicates that the covariate was not included in the global model. DNSR = Daily Nest Survival Rate, DBSR = Daily Brood Survival Rate. FAge = female age, Prec = winter precipitation, Temp = winter temperature, Nage = nest age, Bage = brood age, Date = nest initiation date or hatching date for the brood survival.

precipitation (Fig. 2).

Removing the nest initiation date covariates from the breeding parameters analysis only revealed a steeper significant additive effect of the age on clutch size (see Supplementary Appendix M).

4. Discussion

Our results for the breeding parameters of captive-bred female Houbara in the wild indicate that age dependence in breeding performance varies with both the parameter considered and environmental conditions. We showed that while all parameters exhibited markedly lower performance at young ages compared to adulthood, only a subset of these had a senescence pattern.

4.1. Intra-seasonal variation in breeding performances

Temporal and longitudinal changes in performance during the nesting and brooding periods can drastically affect the estimation of

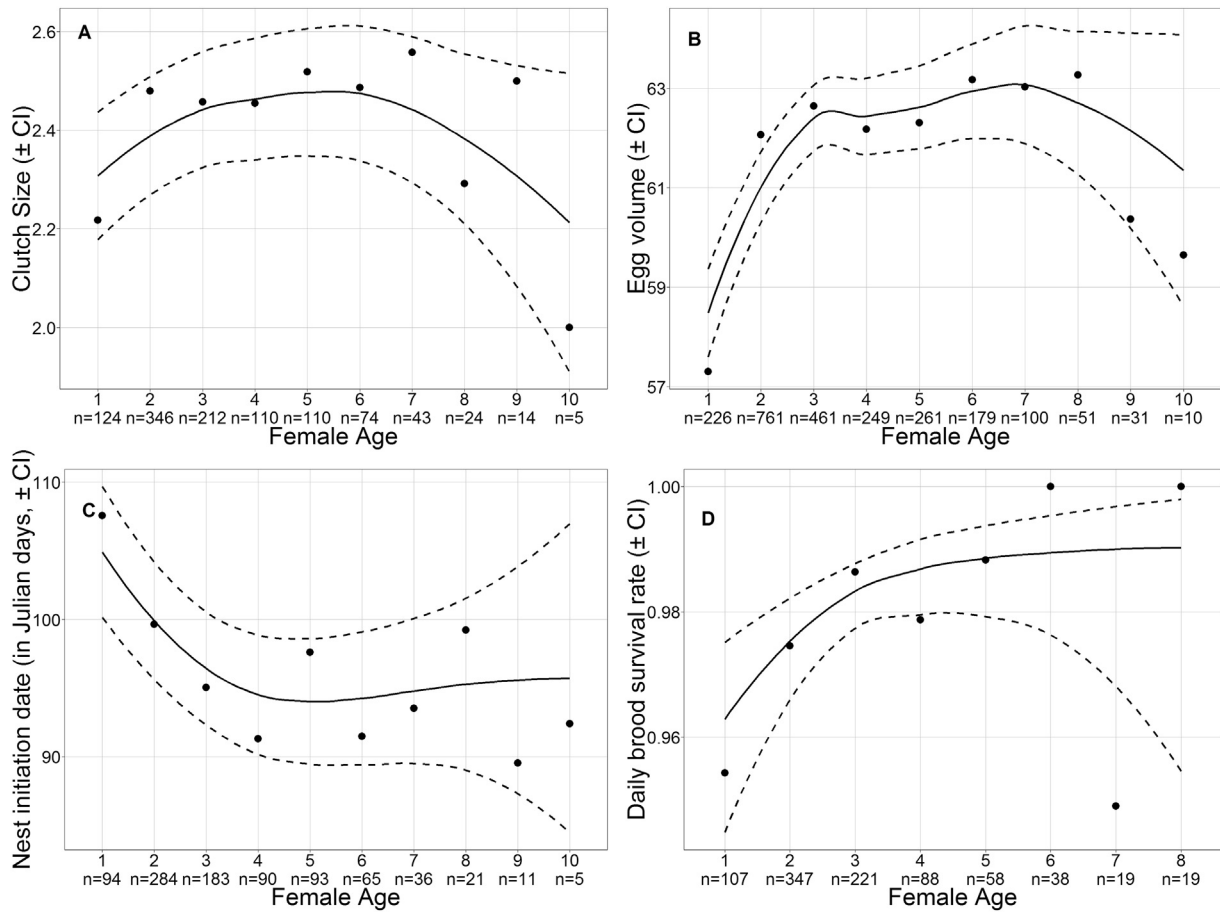


Fig. 1. GAMM predictions (lines and dashed lines for \pm 95% CIs) and observed average values (points) of the clutch size (A), egg volume (B), nest initiation date (C), and daily brood survival rate (D) as functions of the age of the nesting female.

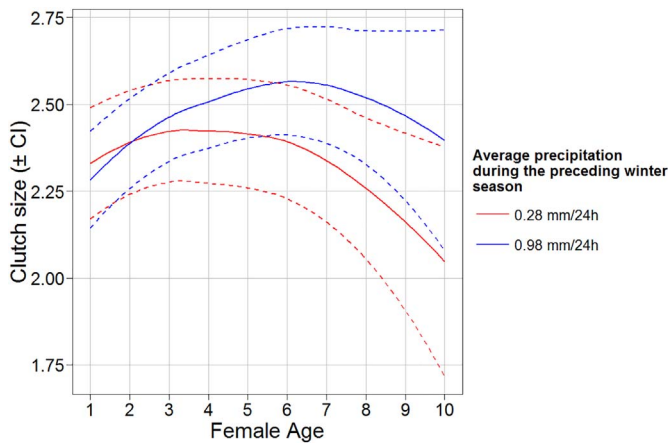


Fig. 2. GAMM predictions (lines and dashed lines for \pm 95% CIs) as functions of the age of nesting females with low average winter precipitation (in red, first quartile, 0.28 mm/24 h) and high average winter precipitation (in blue, third quartile, 0.98 mm/24 h) preceding the breeding season (from December to February).

daily survival rates (Grant and Shaffer, 2012). Here, nest and brood ages had significant effects on daily survival rates (Table 1). Nest survival rate decreased with the age of the nest, while brood survival increased with the age of the brood, and the most important period for the breeding success of females occurred between nesting and brooding, i.e., at the transition between the hatching and the exodus of the chicks (Supplementary Appendix L, Fig. L).

Camera traps indicated that 74% of nest failures were caused by

predation and that at least 90% of nest predation events were caused by mammals, especially the red fox (*Vulpes vulpes*). Scent trails (Clark and Wobeser, 1997) and increasing female activity (Martin et al., 2000) at the end of the incubation stage, when chicks are pipping, may increase nest detectability, especially from mammalian predators (Martin et al., 2000; Fields et al., 2006).

Concerning brood survival, the increasing daily survival with the brood age is related to the increased mass and movement capacity of chicks, positively affecting their survival (Combreau et al., 2002). In contrast to eggs in the nest, chicks progressively become independent from each other so that the failure of the whole brood (i.e., all chicks dead) becomes less likely with time.

4.2. Meteorological effects

Our results indicate that nest survival increases with the amount of precipitation received during the winter preceding the breeding season. In arid environments, precipitation patterns have critical effects on primary production and resource availability (Gamoun, 2016). This in turn influences breeding performance (Morrison and Bolger, 2002). In particular, greater resource availability and quality may allow nesting females to avoid lengthy foraging trips, reducing nest detectability and thus vulnerability from predators (Schmidt, 1999; Martin et al., 2000) and allowing an increased ability to cope with the energy demands of incubation (Weimerskirch et al., 2012). Additionally, higher primary and secondary productivity following high amounts of precipitation in winter may increase the abundance of alternative prey for predators, decreasing nest predation (Schmidt, 1999). Similar positive effects of precipitation on nest survival at the inter-annual scale have been

observed in other avian species inhabiting arid and semi-arid environments, for example, the rufous-crowned sparrow (*Aimophila ruficeps*, Morrison and Bolger, 2002) and the great bustard (*Otis tarda*, Morales et al., 2002).

4.3. Breeding parameters of young females and initiation date

Most breeding parameters (except for nest survival, see Supplementary Appendix N) consistently showed age-specific variation, suggesting an increase in breeding performance in young females (from 1 to 3 years of age, Fig. 1).

For many bird species, it has been generally observed that females breeding earlier in the season have greater breeding success (Price et al., 1988; Bacon et al., 2017). This pattern is expected with respect to both demographic heterogeneity (high-quality females tend to lay early in the season and have high breeding success independent of their laying date, Christians et al., 2001) and to meteorological changes along the season affecting breeding investment (Zhu et al., 2012). Our results are consistent with this complex relationship between demographic heterogeneity, success and nest initiation date. Using the age of the female as a potential source of demographic heterogeneity, we showed that (1) younger females lay later than others; (2) within a given age class, early-laying females perform better than late-laying females (for all breeding parameters except brood survival, with the exception presumably due to a lack of statistical power). Previous studies concerning age effects on fitness-related parameters showed that demographic heterogeneity related to individual age is manifested indirectly through the timing of breeding (Blums et al., 2002; Hatch and Westneat, 2007). Here, the similarity of model-averaged coefficients, whether including the nest initiation date or not, suggests that timing and direct female age effects on breeding performances are not mutually exclusive.

4.4. Reproductive senescence

As mentioned earlier, senescence has for decades been wrongly believed to not occur in wild populations for both conceptual and technical reasons. The main conceptual reason is that according to the early evolutionary theories of senescence (Medawar, 1952), extrinsic mortality rates in the wild should eliminate older individuals before the effects of senescence are measurable (see Nussey et al., 2013 for discussion). More technically, statistical inference of senescence patterns in the wild requires large, individual-based longitudinal datasets, which have become available only recently (Nussey et al., 2008). The assessment of senescence patterns in translocated populations is especially challenging because (1) sample sizes are generally low; (2) accurate long-term demographic monitoring is generally lacking; (3) in several taxa, translocated individuals have been shown to suffer demographic costs of survival and/or breeding parameters (Sarrazin et al., 1996; Hardouin et al., 2014), which may complicate the assessment of age-dependent breeding parameters and further reduce the probability that individuals reach senescent ages.

Here, the study of egg volume and clutch size, which are both strongly related to physiological processes (Williams, 2001; Christians, 2002), revealed characteristic bell-shaped patterns as a function of age, in concordance with both theoretical expectations (Kirkwood and Austad, 2000) and empirical results obtained in many vertebrate species (Nussey et al., 2013). These results are also consistent with the results obtained with captive Houbara (Preston et al., 2015). In captivity, the senescence of egg production observed at the phenotypic level was demonstrated to be linked to an increase in genetic variance of the trait for oldest individuals (Chantepeie et al., 2015), in agreement with evolutionary-based senescence theories (Charlesworth, 1994; Williams et al., 2006).

While our results indicate that the phenotypic patterns of physiological degeneration at older ages observed in captivity can be observed

in natural conditions for some breeding parameters, they also suggest that other parameters are not affected by senescence. Many previous studies reported no evidence for senescent trends in fitness related characters in the wild. Nisbet and Dann (2009) did not observe senescent trends in nest initiation dates of little penguins (*Eudyptula minor*), and no age-related decline of reproductive success was observed in the snow petrel (*Pagodroma nivea*, Berman et al., 2009). The lack of senescent patterns for certain breeding parameters may be explained by the improvement of female experience with age and interactions with external factors such as predation, which is one of the main causes of nest failure (Martin, 1995).

4.5. Environmental variation and age of females

Our results show that in young females, clutch size is consistently small regardless of winter precipitation patterns, while the clutch size of older females is only higher after winters with high precipitation (Fig. 2). Scarcity and high variability in resource availability may lead female Houbara to maintain basal reproductive investments in years with low precipitation. Higher winter precipitation and in turn higher primary and secondary spring productivity may contribute to good physiological conditions in females, increasing their reproductive effort through the number of eggs laid (Morales et al., 2002). However, independently of precipitation patterns, young individuals may keep their investment below a maximum level to maximize future reproduction (Curio, 1983). These lower performances could be even more marked in our case, as young captive-bred released females may require time to adapt to their new environment and to reach foraging capacity before investing more in reproduction.

Some previous studies in long-lived animals have hypothesized that the sensitivity of individuals (in relation to survival and/or reproduction) to harsh environmental conditions is higher for some categories of individuals, including young (Fay et al., 2017) and senescent (Reichert et al., 2010; Chantepeie et al., 2016) individuals. Our analysis uncovers the opposite patterns in Houbara, suggesting that some components of the demographic heterogeneity (here, the difference between very young and adult females in terms of clutch size) become more apparent under favourable conditions (Robert et al., 2015b).

5. Applications and perspectives

Overall, our study indicates that individual age is a significant component of demographic heterogeneity for captive-bred Houbara translocated in the wild. These results agree with theoretical expectations and empirical results found in non-translocated populations (Chantepeie et al., 2015; Preston et al., 2015). We argue that the assessment of age dependence, and in particular senescence, in demography is highly valuable to the understanding and successful diagnosis of translocated populations, for several reasons. First, fundamental evolutionary knowledge in life history traits and demography is a prominent driver of conservation research at the population level. Recently, the study of senescence has become more and more standard in population ecology (Nussey et al., 2008, 2013). It is important that the consideration of senescence becomes standard in conservation as well to strengthen synergies among basic ecology and conservation.

Second, because senescence is the final stage of the life history, the observation in translocated individuals of senescence patterns like those observed in free-ranging, non-translocated populations may indicate that the individual life history of released animals is not strongly modified or truncated by translocation protocols. This result has strong implications for translocation programmes potentially associated with release costs and phenotypic changes affecting the life histories of released individuals.

Finally, accurate assessment of the success of conservation translocation programmes requires precise quantification of the long-term viability of translocated populations, ideally based on quantitative

population viability assessments (Robert et al., 2015c). Because senescence has recently been shown to affect the growth rate and viability of populations in the wild (Robert et al., 2015a; Chantepie et al., 2016), our results imply that senescence is an important constraint to consider in the process of assessing the feasibility and success of conservation translocations.

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Supplementary material

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.08.023>.

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Supplementary materials – Article 1

Appendix A. Location of the intervention area of the Emirates Center for Wildlife Propagation in Eastern Morocco

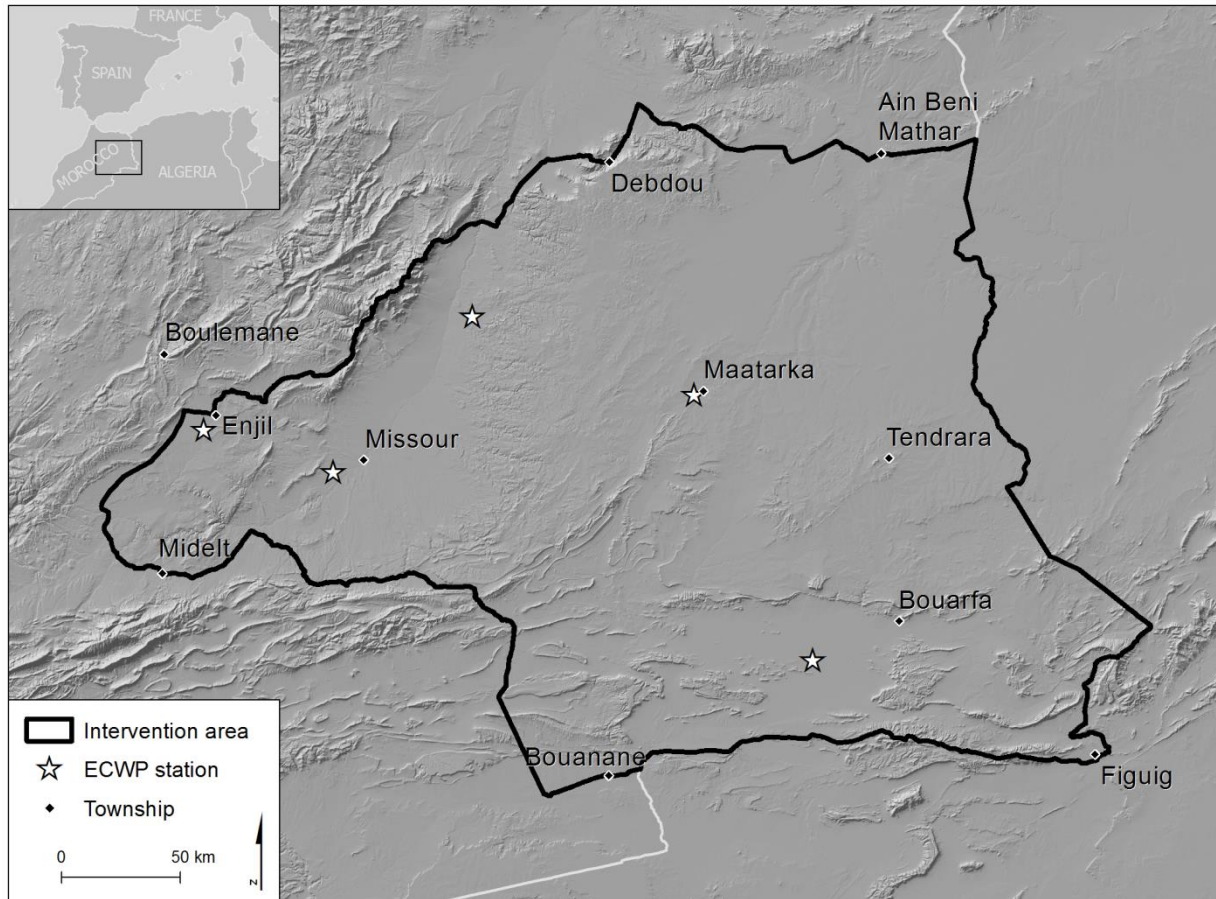


Figure A. Location of the intervention area of the Emirates Center for Wildlife Propagation in Eastern Morocco.

Appendix B. Marking of released individuals and nesting females identification

Prior to 2006, released Houbara were tagged on the left tarsus with an aluminium ring displaying a unique ID number. Since 2006, all released individuals have been subcutaneously microchipped with a unique Radio Frequency IDentification (RFID) tag (TROVAN LID100 implantable transponder, DorsetID; see Hardouin et al. 2015). In Eastern Morocco, 3014 released birds were equipped with transmitters (1937 with VHF transmitters, 933 with satellite transmitters and 144 with GSM transmitters). In addition, some released females were recaptured in the wild and fitted with VHF (11 females) or satellite (29 females) transmitters. See Hardouin et al. (2015) for details on the trapping method.

Over the study period, 167 females from 332 nests were identified from their fitted VHF transmitters, 48 females from 72 nests from their PTT/GSM transmitters and 33 females from 33 nests were identified during their capture based on their rings and RFID tags.

In addition, starting in 2013 (locally tested in 2011 and 2012), specifically designed RFID readers were used to identify nesting females tagged with a RFID tag. The reader is composed of a square or octagonal shaped antenna that surrounds the nest, plugged to a decoder unit powered with a 12V battery. When the female sits on the antenna, it supplies energy to the implemented RFID tag, and receives a unique ID-code that is transmitted to the decoder. We deployed the system on the nests, where it was left for approximately two hours, to let the female come back onto the nest. If sightings conditions were favourable, an observer could check for the return of the female onto the nest, placed at a distance of 700 to 1000 m, using a telescope. The whole system was camouflaged, with double sided tape covered in sand on the antenna and camouflage netting and naturally occurring materials on the decoder unit and the battery. To assess that females were returning to incubate the eggs on the antenna, camera traps were placed close to the nests while the set-up was deployed (see details on camera traps in online appendix E). Using RFID readers, we identified 580 nesting females on 657 nests. During our study period, we didn't observe significant overall deleterious effect of RFID readers on the daily nest survival rate.

Appendix C. Nesting and brooding females sample size details

Table C.1. Total nest sample size with respect to the age of nesting females and the year of nesting.

Years	Age of nesting females										Sum
	1	2	3	4	5	6	7	8	9	10	
2002	10	3	0	0	0	0	0	0	0	0	13
2003	1	9	1	0	0	0	0	0	0	0	11
2004	15	19	18	2	0	0	0	0	0	0	54
2005	0	1	6	4	2	0	0	0	0	0	13
2006	16	25	8	2	0	1	0	0	0	0	52
2007	5	21	6	4	4	4	3	0	0	0	47
2008	0	45	9	1	2	2	2	3	0	0	64
2009	3	1	1	5	0	0	0	1	2	0	13
2010	2	15	0	4	3	0	0	0	1	0	25
2011	7	9	3	2	0	0	0	0	0	0	21
2012	7	16	12	8	8	1	0	0	0	0	52
2013	18	34	51	33	26	4	3	0	1	0	170
2014	5	31	18	24	26	14	7	3	0	0	128
2015	28	80	33	12	31	22	11	9	4	2	232
2016	11	41	53	13	13	29	19	10	7	3	199
Sum	128	350	219	114	115	77	45	26	15	5	1094

Chapitre 1. Preuve de sénescence reproductrice chez les individus lâchés dans une population renforcée.

Table C.2. Total brood sample size with respect to the age of females and year.

Years	Age of brood rearing females								Sum
	1	2	3	4	5	6	7	8	
2002	4	1	0	0	0	0	0	0	5
2003	0	4	0	0	0	0	0	0	4
2004	11	8	9	0	0	0	0	0	28
2005	0	0	2	1	1	0	0	0	4
2006	6	8	7	0	0	0	0	0	21
2007	2	10	4	2	3	1	2	0	24
2008	0	22	4	1	1	1	1	0	30
2009	2	0	1	2	0	0	0	1	6
2010	1	8	0	2	1	0	0	0	12
2011	3	1	1	0	0	0	0	0	5
2012	1	3	2	2	0	0	0	0	8
2013	1	0	3	0	0	0	0	0	4
2014	0	0	1	0	0	0	0	0	1
Sum	31	65	34	10	6	2	3	1	152

Appendix D. Nests visits per year

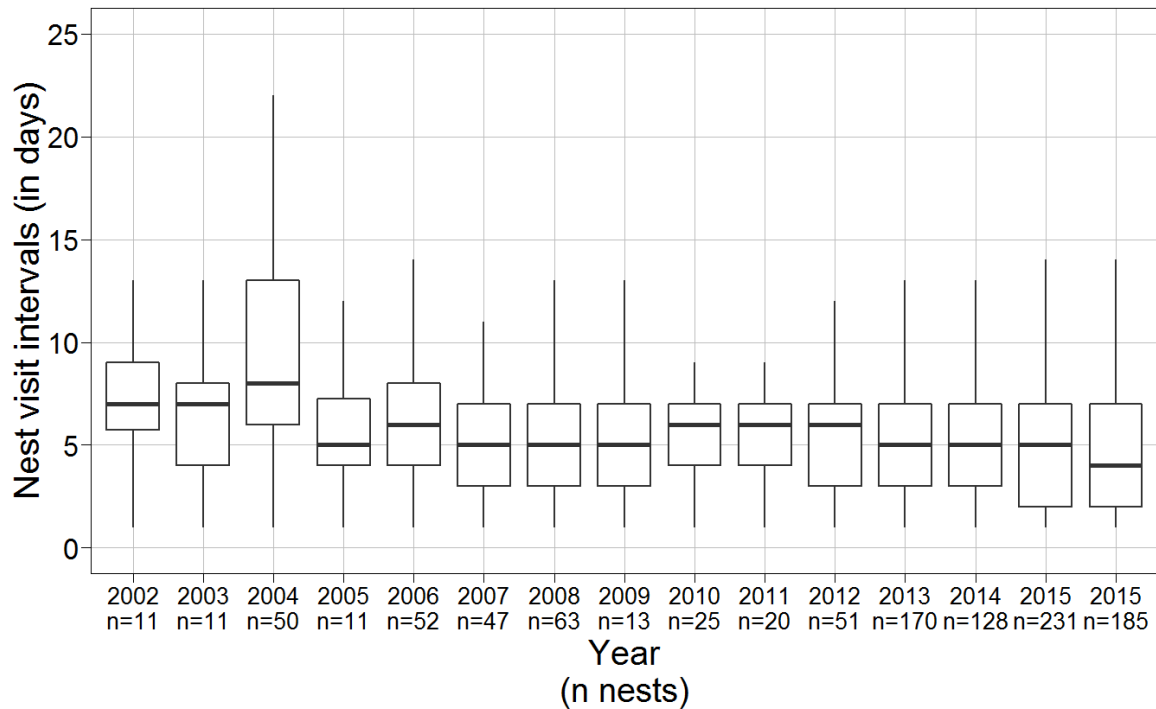


Figure D. Nest visit intervals boxplot distribution per year.

Appendix E. Camera trap survey

Camera traps were used to obtain a continuous survey of nests and to assess the return of females on nests where RFID readers were deployed (see online appendix B). We used eight camera trap models from Reconyx (PC900, HC600), Moultrie (Plotstalker, M990i), Scoutguard (SG550, SG580) and UOVision (UM535, MB500). During our study period, we did not observe significant overall deleterious effect of camera traps on the daily nest survival rate.

Appendix F. Egg volume and nest initiation date calculation

From 2003 onwards, the length and width of each egg were measured with a calliper (to the nearest hundredth of cm) and the mass with a spring balance (to the gram) or an electronic balance (to the tenth of gram). The width and length of eggs were then used to calculate the egg volume (Vol) in cm^3 as:

$$\text{Vol} = (0.51 * w^2 * l) / 1000$$

Where 0.51 is the average volume coefficient of an egg calculated from 124 bird species (Hoyt 1979), w the egg width (cm) and l the egg length (cm).

The nest initiation date was estimated from the calculation of the eggs' incubation stage (in days) at the time of measurement (Combreau et al. 2002, Hoyt 1979, Saint-Jalme & van Heezik 1996). The egg incubation stage (IS) was calculated as:

$$IS = 23 * (W_f - W) / (W_f - W_p)$$

Where W_f is the fresh weight of the egg, calculated from the mass specific coefficient of the Houbara egg ($Kw = 0.55$, Combreau et al. 2002) and the egg dimensions:

$$W_f = Kw * l * w^2$$

W_p is the weight of the egg at hatching (Hoyt 1979). W_p is proportional to W_f and corresponds to the average weight loss in a Houbara egg (17%) during a complete egg incubation (Saint-Jalme & van Heezik 1996). W is the mass of the egg at the moment of measurement.

The nest initiation date was then defined as the date of first egg laid:

$$Nest\ initiation\ date = MD - \bar{IS} - (2.5 * (n - 1))$$

Where MD is the measurement date, \bar{IS} is the mean incubation stage from the eggs measured at the date of measurement and n the clutch size. The mean interval between two eggs laid is assumed equal to 2.5 days (Gaucher 1995). Then, we were able to estimate the nest age (in days) at each visit.

Appendix G. Sample size differences for breeding parameters related to the nest.

The sample sizes of the datasets varied among breeding parameters. Explanations and justifications are provided below.

Overall, captive-bred females were identified on 1094 nests between 2002 and 2016.

Thirteen nests were found within the fenced enclosures of ECWP centers and were not included in the datasets, as environmental conditions were different from outside these areas.

Clutch sizes were not available for twenty nests. Sixteen of these were nests located from females fitted with transmitters and that were empty at the first visit. The last three were nests for which we were unsure about the clutch size.

From the clutch size dataset (1062 nests), egg volumes were not available for 88 nests. For 85 nests, no egg measurements were made. For the three remaining nests left, one had abnormal egg measurements and two had egg measurements made while the eggs were pipping.

Nests initiation dates (882 nests) were estimated from egg measurements (974 nests). For one nest, the eggs mass measurements were missing. The calculation of the incubation stage of eggs is very sensitive to mass measurement errors, so to be conservative we decided to exclude biologically aberrant data. It was observed in the wild (Bacon and Hingrat, unpublished data) that the incubation time for hatching eggs ranged between 19 days and 31 days. Based on these observations, we excluded eggs with aberrant incubation stages (negative incubation stages, maximum incubation stages > 31 days; which represented a total of 72 nests). We also excluded nests for which we had doubts on the viability of the whole clutch (n=19), because the female incubated the eggs for over 31 days without any egg hatching. Estimating incubation stage on unfertile eggs or dead eggs may be biased because the water loss of these eggs is different from that of fertile eggs with embryo development.

The nest survival dataset sample size (867 nests) could not be larger than the nest initiation date dataset sample size as the nest age covariate was calculated on nest initiation dates. Furthermore, fifteen nests were not implemented in nest survival analysis because they were visited only once or because the status of the nest was unknown at the first visit. A minimum of two visits (for one time interval) is necessary to implement the data in logistic exposure survival models.

Appendix H. Nest and brood Survival analyses

We used the logistic exposure approach of Shaffer (2004) to estimate the daily nest survival rate (probability of a living nest to not fail in one day, Mayfield 1975). This method uses a generalized linear mixed effects model (GLMM) with a binomial probability distribution, and a custom logit link function that performs with variable exposure periods between nests visits. For hatching nests, exposure periods stopped when the first egg hatched. If the exact hatching date was not known, it was estimated as the mid-date of the interval between the last visit with intact eggs and the first visit with at least one hatched egg (Manolis et al. 2000). For

nests with an unknown final fate or influenced by observers (n=1), the exposure period was right-truncated at the last visit for which the nest was known to be active. This approach does not require the exact day of nest failure but the interval within which the failure occurred. As recommended by Grant & Shaffer 2012, we included the nest age (calculated from nest initiation dates) as a covariate in the daily nest survival analysis. Therefore, nests without known nest initiation date were excluded from this analysis (see appendix G for sample sizes).

The same statistical approach was used to study brood survival, with the exception that the exposure period of successful broods ended at 60 days (Combeau et al. 2002, Hardouin et al. 2012) and we did not include broods with an unknown final fate (n=26), based on a personal communication with Stephen Dinsmore (see discussion in Manolis et al. 2000). Because the age of a given brood is mandatory to evaluate its success, we considered the life history of broods to start at the hatching date. Thus, contrary to nests, all broods started at the same age. Integrating broods with an unknown final fate (i.e., broods for which the daily survival history is right-truncated) may complicate and bias our results, especially if the daily brood survival varies with the age of the brood (Combeau et al. 2002).

Appendix I. Covariate effects studied for each breeding parameter.

Table I. Additive, quadratic and interaction effects from the covariates studied for each breeding parameter.

Covariates	Breeding parameters					
	Nest date	initiation	Clutch size	Egg volume	Daily nest survival rate	Daily brood survival rate
Female age	X		X	X	X	X
Female Age ²	X		X	X	X	X
Nest initiation date	-		X	X	X	-
Hatching date	-		-	-	-	X
Nest age	-		-	-	X	-
Nest age ²	-		-	-	X	-
Brood age	-		-	-	-	X
Brood age ²	-		-	-	-	X
Precipitation winter season	X		X	X	X	-
Temperature winter season	X		X	X	X	-

“X” indicate that the effect is included in the analysis ; “-“ indicate that the effect is not included in the analysis

Appendix J. Average temperature (°C) and precipitation (mm/24h) during the winter season (from December to February) from 2002 to 2016.

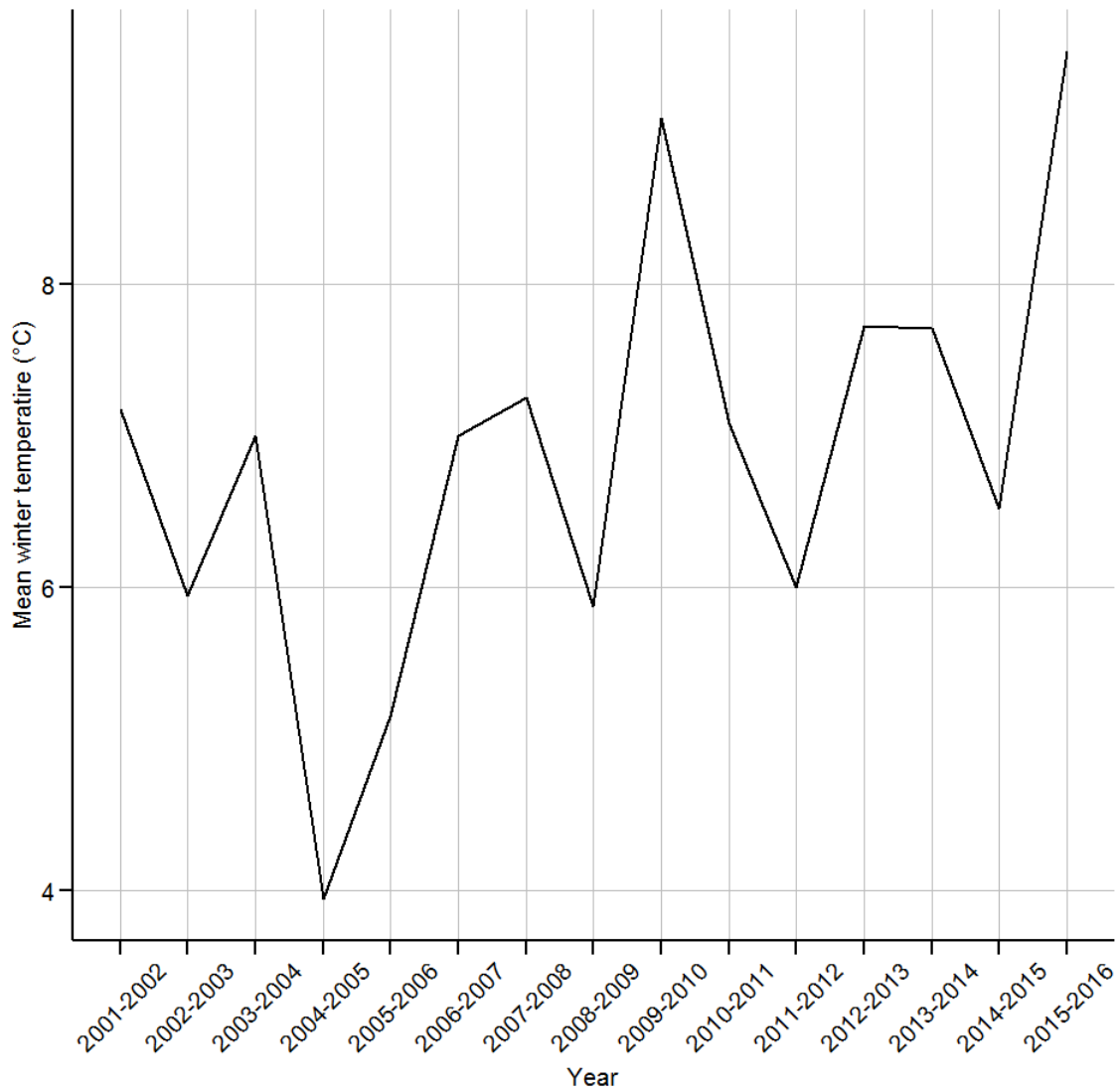


Figure J.1. Average temperature (°C) during the winter season (from December to February) preceding the breeding season.

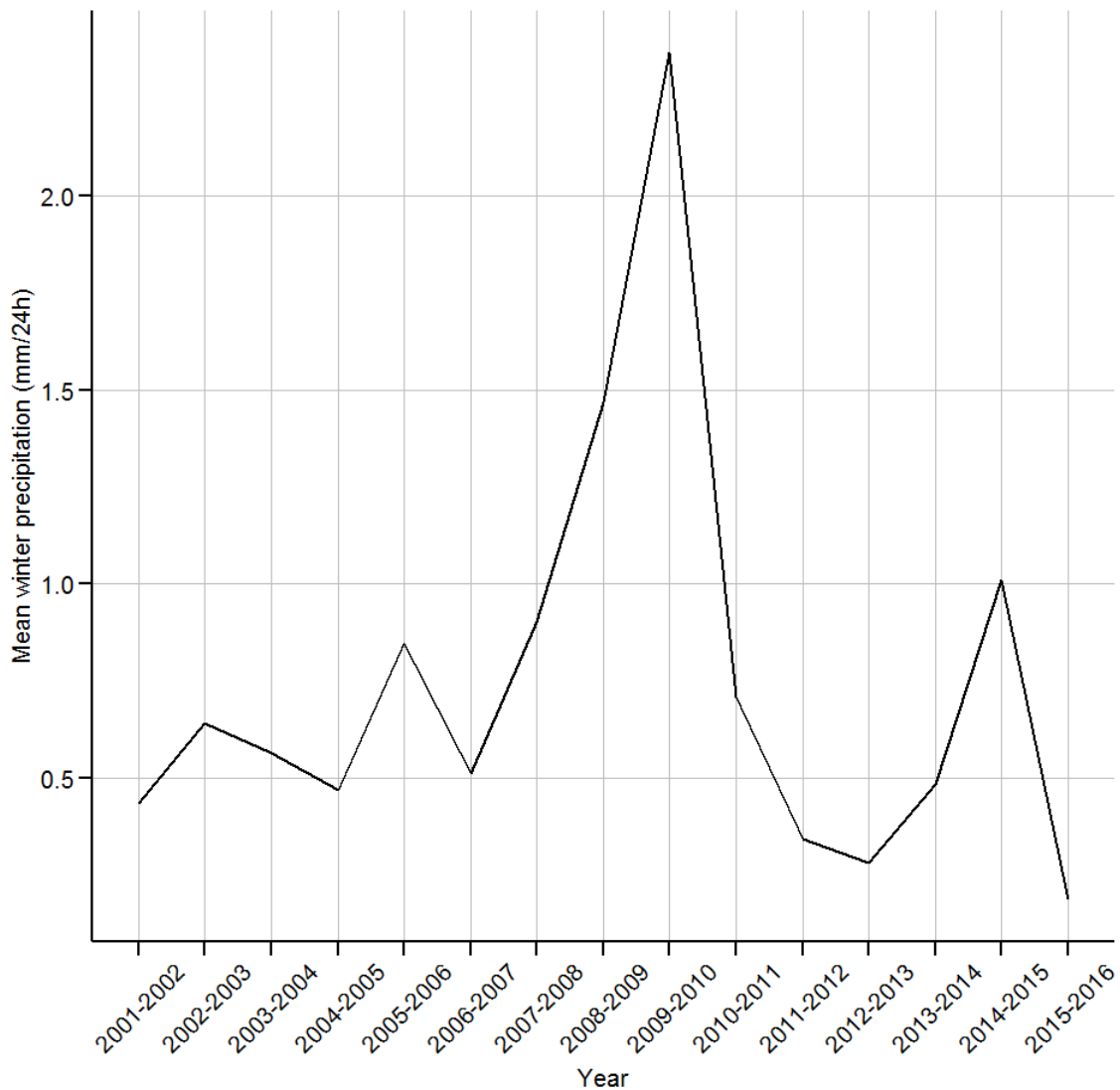


Figure J.2. Average precipitation (mm/24h) during the winter season (from December to February) preceding the breeding season.

Appendix K. Clutch size analysis using linear mixed models (LMMs) fitted by maximum likelihood with a Gaussian distribution and an identity link function

We used Generalized Additive Mixed Effects Models (GAMMs) to assess the shape of the main effect of the female age on breeding parameters with significant model averaged age effects. Because ordinal regressions with random effects are not implemented in GAMMs yet, we predicted the clutch size as a function of the female's age using GAMM assuming a Gaussian distribution. We are confident that this approach does not lead to strong bias of graphical predictions because multi-model inference of the clutch size using Gaussian LMMs yielded similar results as the more robust CLMM (Cumulative Linked Mixed Models) analysis (see Table K below and Table 1 in the main manuscript).

Table K. Model-averaged additive, polynomials and interactions effects coefficients (\pm 95% CIs) from the set of best models of the clutch size analysis using linear mixed models (LMMs) fitted by maximum likelihood with a Gaussian distribution and an identity link function.

Covariates	Estimate	Lower CI	Upper CI
Fage	0.14	0.04	0.23
FAge ²	-0.17	-0.29	-0.06
Date	-0.29	-0.36	-0.23
Prec	0.07	-0.09	0.23
Temp	-0.05	-0.23	0.13
FAge x Prec	0.19	0.06	0.33
FAge x Date	0.10	-0.02	0.22

FAge = female age, Prec = winter precipitation, Temp = winter temperature, Date = nest initiation date.

Appendix L. Temporal variation of the daily survival rate as a function of the age of the nest and age of the brood.

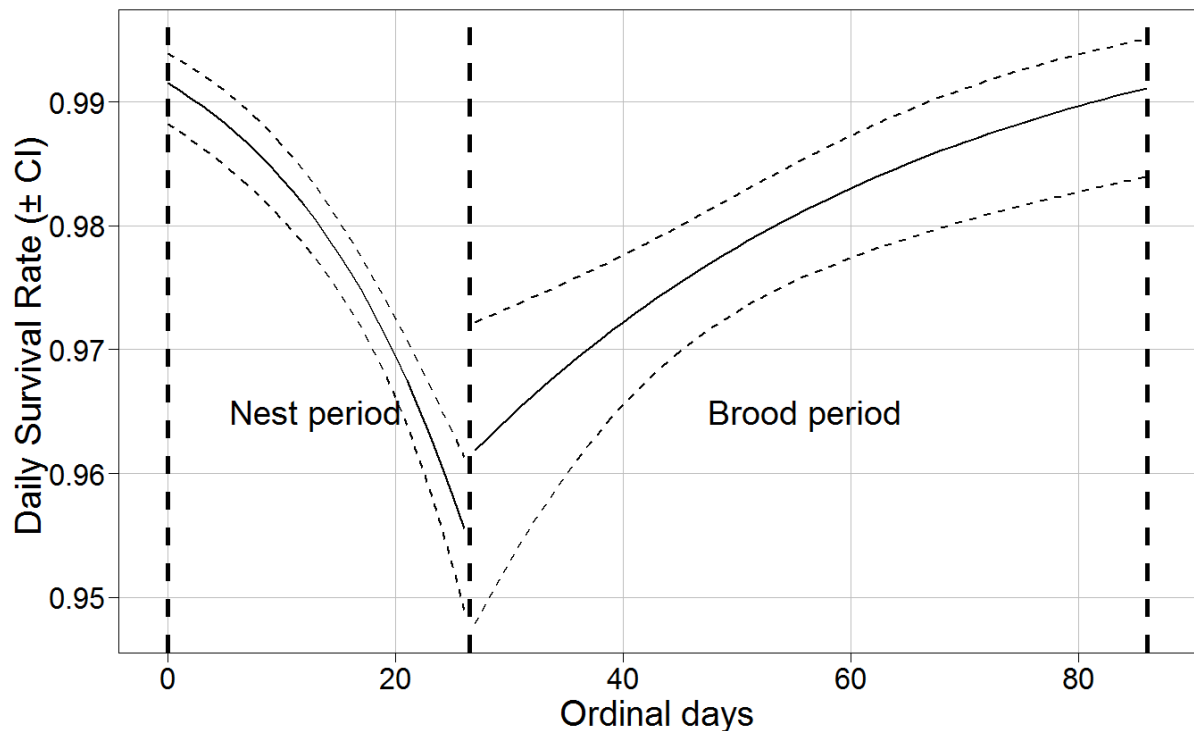


Figure L. Temporal variation of the daily survival rate (\pm 95% CIs) as a function of the age of the nest (nest period) and age of the brood (brood period).

Appendix M. Breeding parameters analysis without consideration of the nest initiation date

Chapitre 1. Preuve de sénescence reproductrice chez les individus lâchés dans une population renforcée.

Table M. Model-averaged coefficients (\pm 95% CIs) of covariates from the two sets of best models for all breeding parameters. 1. The first analysis focuses on the additive effects of covariates. 2. The second analysis includes additive, quadratic and interaction effects.

Covariates	DNSR	DBSR	Clutch size	Egg volume
1. Additive effects (first set of candidate models)				
Fage	0.19 [-0.04, 0.41]	0.85 [0.18, 1.52]	0.32 [0.04, 0.60]	1.66 [0.98, 2.34]
Prec	0.29 [0.05, 0.53]	-	0.23 [-0.42, 0.89]	-0.06 [-0.82, 0.70]
Temp	-0.07 [-0.32, 0.17]	-	-0.15 [-0.90, 0.61]	0.36 [-0.40, 1.13]
Nage	-0.96 [-1.19, -0.73]	-	-	-
Bage	-	0.72 [0.11, 1.34]	-	-
2. Additive, quadratic and i effects (second set of candidate models)				
FAge ²	-0.08 [-0.45, 0.30]	-0.75 [-1.56, 0.05]	-0.95 [-1.39, -0.50]	-2.87 [-3.82, -1.92]
Nage ²	-0.10 [-0.48, 0.28]	-	-	-
Bage ²	-	-0.49 [-1.65, 0.66]	-	-
FAge*Prec	-0.13 ; [-0.91, 0.66]	-	0.76 [0.23, 1.29]	Not selected
FAge*Temp	-0.46 ; [-1.03, 0.11]	-	Not selected	Not selected
FAge*Nage	-0.23 ; [-0.72, 0.26]	-	-	-

Averaged coefficients of additive effects are not presented in analysis 2 because the use of model averaging techniques to assess additive effects is irrelevant when quadratic and interaction effects are presents. Coefficients are in bold, where 95% CIs do not include zero. “Not selected” indicates that the covariate was not selected in the best set of models and “-” indicates that the covariate was not included in the global model. DNSR = Daily Nest Survival Rate, DBSR = Daily Brood Survival Rate. FAge = female age, Prec = winter precipitation, Temp = winter temperature, Nage = nest age, Bage = brood age, Date = nest initiation date or hatching date for the brood survival.

Appendix N. Observed daily nest survival age (\pm 95% CIs) as a function of the age of the nesting female.

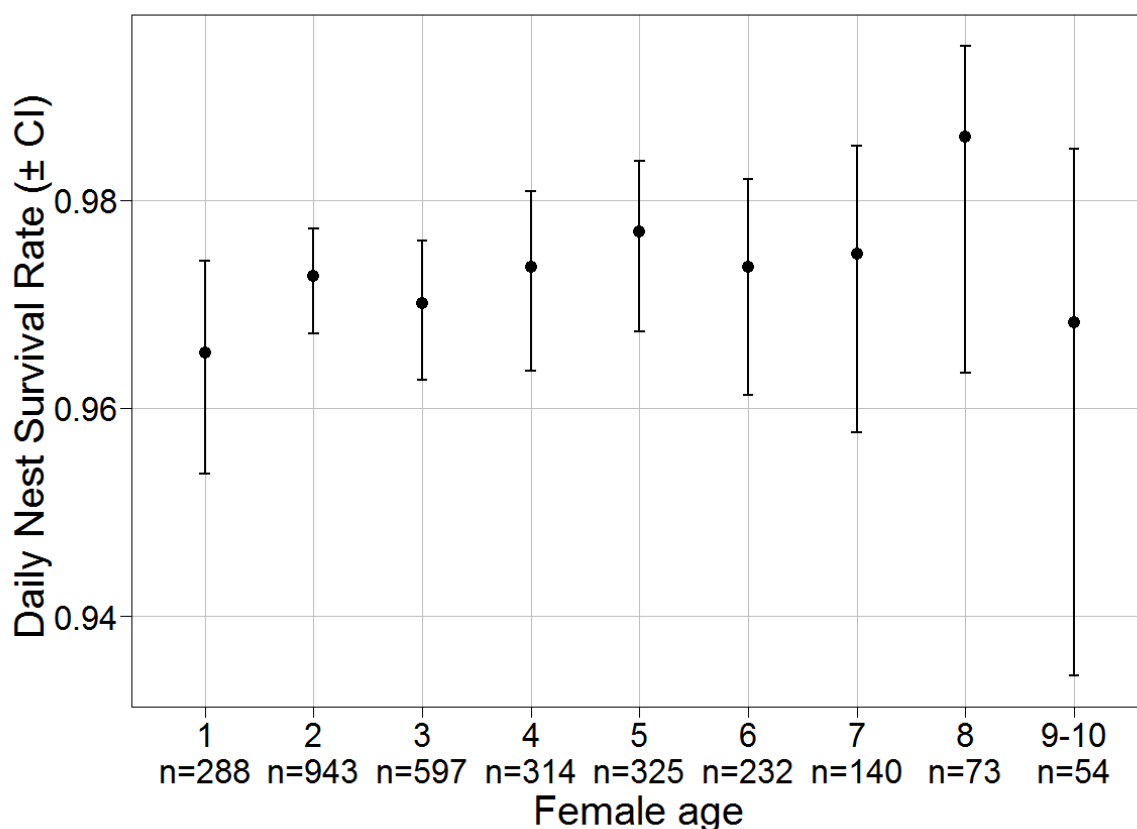


Figure N. Observed daily survival rate (\pm 95% CIs) as a function of the age of the nesting female.

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Chapitre 1. Preuve de sénescence reproductrice chez les individus lâchés dans une population renforcée.

Chapitre 2. Evaluation du coût au lâcher dans une population renforcée : une question de stratégie de lâcher

Résumé

Le succès d'un programme de translocation conservatoire est fortement lié à la démographie des individus lâchés et en premier lieu à leur capacité à survivre et à se reproduire dans leur nouvel environnement. Pour de nombreux programmes de translocation d'animaux, il a été observé que les individus lâchés ont des performances démographiques inférieures à celles de leurs congénères nés à l'état sauvage. Cependant, dans la mesure où les inférences sont généralement faites au niveau de la population (et non au niveau individuel), il reste difficile de comprendre comment l'âge et les effets de la gestion expliquent ce coût au lâcher et si celui-ci est temporaire ou permanent. Dans cette étude, nous avons étudié les potentiels coûts au lâcher sur six paramètres de reproduction d'outardes Houbara nord-africaines produites en captivité et lâchées dans la nature ($n = 204$) en les comparant à des congénères nés à l'état sauvage ($n = 101$). L'âge des individus a été pris en compte et certains individus ont été suivis sur plusieurs années. Nous avons également étudié comment la période de lâcher (lâchers d'automne *versus* de printemps) peut affecter les performances reproductrices des individus produits en captivité. Nos résultats indiquent que (1) les femelles produites en captivité se reproduisent avec succès dans la nature. Cependant (2) pour trois des six paramètres de reproduction étudiés, les femelles lâchées ont des performances inférieures à celles des femelles nées à l'état sauvage. (3) Bien que nous observions des effets de l'âge suggérant une augmentation des performances reproductrices avec l'âge, nous n'avons pas découvert d'interaction entre l'âge et l'origine des femelles. (4) La réduction des paramètres de reproduction dépend de la période de lâcher avec une réduction plus marquée pour les femelles lâchées au printemps. Dans l'ensemble, notre étude montre la capacité des femelles produites en captivité à se reproduire dans la nature et à contribuer à la dynamique de la population au-delà de leur histoire individuelle. Nos résultats révèlent également des coûts au lâcher complexes, mais suggèrent que ces coûts peuvent être minimisés via une stratégie de translocation appropriée.

Mots-clés : Translocation, renforcement, coût au lâcher, reproduction

Note: Contrairement aux analyses des articles 1 et 3, où les résultats sont basés sur les coefficients moyennés d'un ensemble de modèles ($\Delta AICc < 2$), les résultats du chapitre 2 se basent sur les coefficients estimés du meilleur modèle ($\Delta AICc = 0$). Pour plus de détails et explications, voir Annexe 2.

Chapitre 2. Evaluation du coût au lâcher dans une population renforcée : une question de stratégie de lâcher

Article 2. Evaluating the cost of release in a translocated population: a matter of release strategy

Bacon Léo, Robert Alexandre, Hingrat Yves

Article en préparation pour *Biodiversity and Conservation*

Chapitre 2. Evaluation du coût au lâcher dans une population renforcée : une question de stratégie de lâcher

Evaluating the cost of release in a translocated population: a matter of release strategy

Léo Bacon^{a, b, *, **}, Alexandre Robert^b, Yves Hingrat^{a, c}

^aEmirates Center for Wildlife Propagation, PO Box 47, 33250 Missour, Morocco

^bCentre d'Ecologie et des Sciences de la CONservation (CESCO UMR 7204), Museum National d'Histoire Naturelle, CP 135, 43 rue Buffon, 75005 Paris, France

^cRENECO International Wildlife Consultants LLC., Po Box 61741, Abu Dhabi, U.A.E.

*Corresponding author (bacon.leo@gmail.com)

**Orcid ID: 0000-0003-1200-9902

Key-words: Translocation, reinforcement, cost of release, reproduction

Abstract

The success of conservation translocation programmes is critically related to the demography of translocated individuals and particularly to their ability to survive and reproduce in their new environment. In many animal translocation programmes, it has been observed that translocated individuals have lower demographic performances than their wild-born conspecifics. However, because inferences are generally made at the population (not individual) level, it remains difficult to understand how age and management effects influence such costs of release, and whether these costs are temporary or permanent. In this study we investigated potential costs of release on six breeding parameters of captive-bred North-African Houbara bustards (*Chlamydotis undulata undulata*) translocated in the wild (n=204) by comparing them to wild-born conspecifics (n=101). The age of individuals was taken into account and some individuals were monitored along their lives over the 15 years of the study. In addition, we investigated if the period of release (autumn *versus* spring releases) affected breeding performances of captive-bred released females. Our results indicate that (1) captive-bred released females successfully breed in the wild. However (2) for three out of six breeding parameters studied, released females have lower performance than wild-born females. (3) Although we observe consistent age effects in performances suggesting an increase of breeding performances at young ages, we did not uncover any interaction between age and the origin of females, suggesting that the reduction of breeding parameters in released

females is long lasting. (4) The reduction of breeding parameters depends on the period of release with more marked reduction for spring releases. Overall, our study supports the capacity of captive-bred females to reproduce in the wild and to contribute to the dynamics of the population beyond their individual history. Our results also uncover complex release costs but suggest that these costs can be minimized through an appropriate translocation strategy.

Introduction

The success of conservation translocation programmes is commonly defined as the capacity of translocated populations to persist without further interventions (Ewen et al. 2012, IUCN 2013). Assessment of success thus requires understanding the long-term dynamics and viability of translocated populations (Robert et al. 2015a), which in first and foremost requires long-term demographic assessment (Sutherland et al. 2010). However, such assessment is rarely achieved mainly due to the lack of appropriate monitoring and difficulties in data analysis (Fischer & Lindenmayer 2000, Sutherland et al. 2010). Translocated populations are complex, heterogeneous and unbalanced systems (Robert et al. 2007) and the assessment of demographic performances is required to encompass this complexity. In particular, it is necessary to assess potential demographic variations among translocated and wild-born organisms.

Previous knowledge indicates that the demography of translocated populations is likely to be affected by a variety of genetic and non-genetic issues. Genetic issues include outbreeding depression (Huff et al. 2011) and ill adaptation (Montalvo & Ellstrand 2001) as well as inbreeding and drift loads (Robert 2009). In cases of translocations based on captive-breeding, adaptation to captivity (Frankham 2008) might be an important additional issue.

In animals, non-genetic issues are associated with the rearing and release strategies leading to various factors potentially affecting demographic rates in the wild: individual condition (health status, physiology and behaviour, Champagnon et al. 2012, Dickens et al. 2010, Hardouin et al. 2014, Tavecchia et al. 2009), proximity of the release site with other populations (Mihoub et al. 2011), period of release (Hardouin et al. 2014), age at release (Sarrazin et al. 1996) or the animal group size and composition (Hardouin et al. 2014, 2015). Then, the potential alteration of demographic performances of translocated individuals might be explained by the interaction of their phenotype with their new environment and release conditions. These reductions have been referred to as release costs (Tavecchia et al. 2009, also named translocation cost or post-release effects, Ewen et al. 2012). These costs have been

defined either as lower performances of translocated individuals relative to wild-born individuals (e.g. Brown et al. 2006) or as lower short term performances of translocated individuals just after release relative to their longer term performances (e.g. Tavecchia et al. 2009, Armstrong & Ewen 2001). A number of studies in translocated vertebrates have documented release costs mostly in terms of survival probabilities (Bertolero & Oro 2009, Hardouin et al. 2014, Tavecchia et al. 2009, Sarrazin et al. 1994), but also in reproduction rates (Sarrazin et al. 1996, Bertolero & Oro 2009) and even in dispersal behaviour (Le Gouar et al. 2008, Mihoub et al. 2011).

However, disentangling the various sources of demographic variation in translocated populations (and in particular those related to the translocation protocol from other sources of variation) is challenging because (1) the comparison between translocated and wild-born animals requires the monitoring of wild-born individuals, a difficult task often hindered by several methodological and ethical issues; (2) short term release costs in translocated individuals can be confounded with other longitudinal sources of demographic heterogeneity such as age effects (Bacon et al. 2017), or by inter-individual heterogeneity (e.g., apparent improvement of survival due to the selection of best survivors).

The North-African Houbara bustard (*Chlamydotis undulata undulata*, hereafter Houbara) is a medium size bird historically distributed from North Mauritania to Egypt, threatened by over-hunting, poaching and habitat degradation, which have led to the decline of the species during the second half of the twentieth century (Goriup 1997). This decline led to the establishment of a reinforcement programme (the Emirates Center for Wildlife Propagation, see Material and Methods) relying on captive breeding, regular releases of captive-bred individuals, combined with ecological research and hunting management, in order to increase the population size of the threatened Houbara throughout its range and to maintain viable populations in adequacy with traditional Arab falconry (Lacroix et al. 2003).

Importantly, captive-bred Houbaras are released as juveniles (within their first year of life) either before or during the breeding season (respectively in autumn and in spring). Previous works on translocated Houbaras indicate that (1) captive-bred juveniles suffer varying short term post release survival, depending on the release season and meteorological conditions, compared to long term survival (Hardouin et al. 2014); (2) one year old released females have reduced breeding performance relative to older released females (Bacon et al. 2017). These results suggest that translocated individuals may experience a short-term (temporary) release

cost. However, in previous assessments of demographic rates, potential short-term release costs may have been confounded with age effects. Thus, a rigorous assessment of the release cost requires formal comparison between release and wild-born individuals of different ages.

Here, we investigate potential differences in breeding performances between wild-born and released captive-bred females, while controlling for age, period of release, temporal and individual effects. We used data collected from a longitudinal nest survey conducted between 2002 and 2016 in the reinforced Houbara population in Eastern Morocco.

We focused on six breeding parameters: nesting effort (number of nesting attempts per breeding season per female), nest initiation date, clutch size, egg volume, daily nest survival and brood survival. We hypothesized that potential short-term release costs exhibited by released Houbaras are related to their potential low conditions and low experience to their new environment (Bertolero & Oro 2007, Bertolero et al. 2009). Thus, potential differences among released and wild-born individuals should decrease with increasing age, reflecting both individual (i.e., gain in experience within an individual, Mauck et al. 2012) and population processes (i.e., death of lower quality individuals, assuming that survival and breeding performance may positively covary, Robert et al. 2015b). We thus predict that:

(1) Within the first year following release, released captive-bred individuals will have lower breeding performances than wild-born individuals of the same age.

(2) One year old individuals released in autumn (i.e., before the breeding season) will be more performant than one year old individuals released in spring (i.e., during the breeding season), as they would have had more time to adapt to their new environment before breeding.

(3) For older individuals (≥ 2), less or no differences in breeding performances will be observed between wild-born and captive-bred females or as a function of the period of release.

Material and methods

Study area

The study was conducted in Eastern Morocco, in the ECWP intervention area (Fig. 1). Cumulating about 50 000 km², the study area is characterized by an arid climate marked by irregular rainfalls (less than 200 mm/year). Mean temperatures vary from 6.80°C in winter

(December to February) to 26.64°C in summer (June to August). The habitat in the study area is characterized by sparse shrubby vegetation.

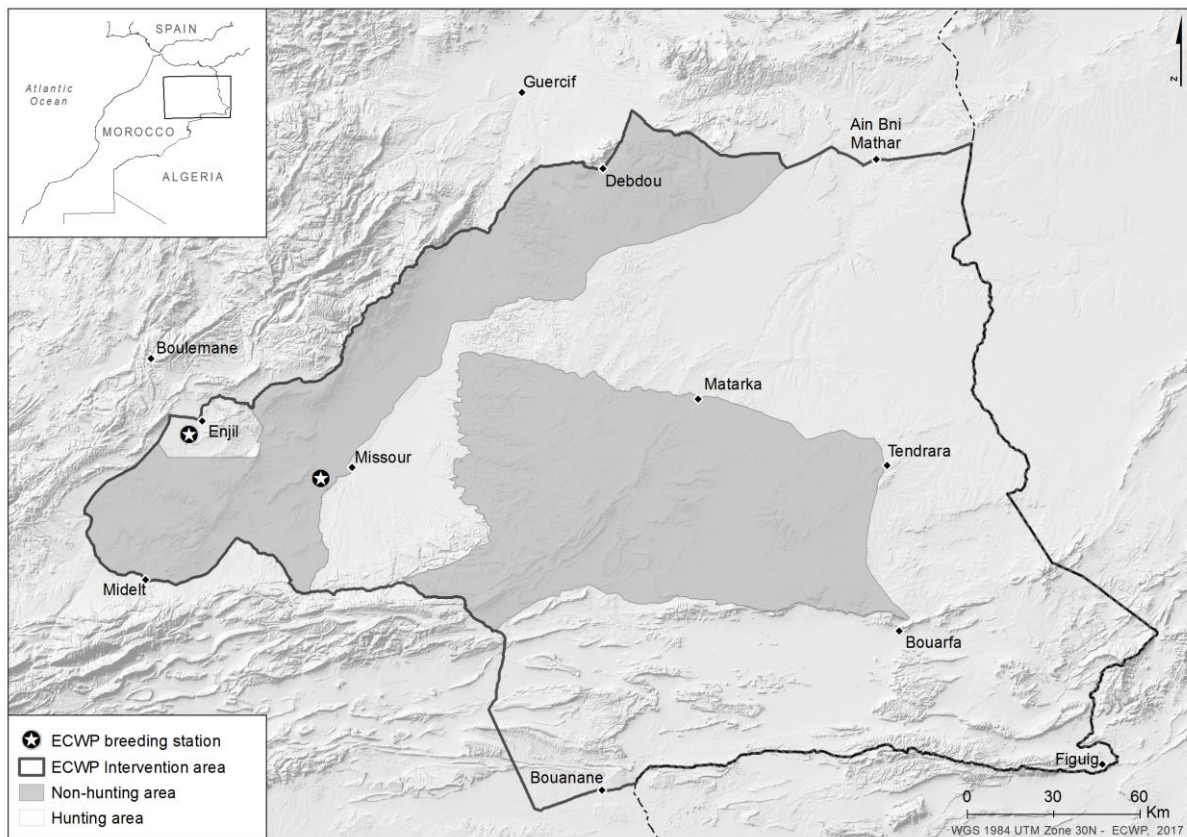


Figure 1. ECWP intervention area partitioned within hunting (30 348 km²) and non-hunting (19 862 km²) areas.

Biological model

The Houbara is a medium-sized bird inhabiting semi-desert steppes of North Africa. It is a ground-nesting, gyneparental incubating species. In Eastern Morocco, females breed from mid-February to mid-June. They lay generally two to three eggs, at 2.5 days interval, which they incubate on average for 23 days (Gaucher 1995). In case of nest failure, females generally initiate a replacement clutch. Houbara chicks are nidifugous but still rely on their mother to be fed during the first 10 days after hatching (Saint Jalme & van Heezik 1996) and fledge at the mean age of 60 days (Hardouin et al. 2012).

Emirates Center for Wildlife Propagation and reinforcement programme

The severe decline of the Houbara population over the last decades led to the establishment of the Emirates Center for Wildlife Propagation in Morocco (ECWP) in 1995. A comprehensive strategy combining reinforcement using captive-bred Houbaras, ecological research, and hunting management was established over the study area. Two ECWP breeding stations were

built for captive breeding (in Missouri in 1995 and in Enjil in 2005, see online appendix A). A detailed description of the captive breeding programme can be found in Lesobre et al. (2010) and Chargé et al. (2010, 2014). Hunting was banned between 2000 and spring 2005 and then restricted to the autumn / winter period (October–January) in 60% of the intervention area. From 1996 to 2016, 108 486 birds were released in North Africa (94 374 in the study area). Within the study area, the overall number of birds released progressively increased over the years (from 28 in 1996 to 9 084 in 2016, see online appendix B), with an increase in the number of release sites and a decrease in the group size per release (Hardouin et al. 2014). The release group size varied between sites (from 4 to 498, median = 18). Houbaras were released at an average of 6 ± 3 (standard deviation) months of age in autumn (August to December), 9 ± 1 months of age in spring (February to May). Autumn releases were managed to avoid direct mortality and disturbance due to hunting. In addition, since 2003, some birds were released in summer (June) at an average of 3 ± 0.6 months of age, but they represent only 8% of total releases in the study area. As such, in this study, we only focused on captive-bred females released in spring and autumn.

Monitoring of captive-bred released females

Prior to 2006, released Houbaras were tagged on the left tarsus with an aluminium ring displaying a unique ID number. From 2006, all released individuals were subcutaneously tagged with a unique radio-frequency identification (RFID) microchip (TROVAN LID100 implantable transponder, DorsetID; see Hardouin et al. 2015 for details). In Eastern Morocco, 3 014 released birds (females 49%) were equipped with transmitters (1 937 with VHF transmitters, 933 with satellite transmitters and 144 with GSM transmitters). The VHF transmitters used in this study were battery-powered necklace units with mortality signals (11 g model RI-2B-M, 20 g model RI-2D-M, Holohil System Ltd., Carp, Ontario, Canada) and solar-powered backpack (19g model Merlin Systems Inc, Boise, Idaho, USA). During the breeding season, females fitted with VHF transmitters were searched at least once a week. The satellite and GSM transmitters used in this study were backpack solar-powered transmitters: PTT-100 30 or 45 g Solar GPS PTT and 30 g solar GSM (Microwave Telemetry, Inc., Columbia, Maryland, USA). To identify breeding events of individuals equipped with satellite transmitters, individuals' movements were checked manually. When stationary locations were recorded, the last location was checked in the field to confirm whether the individual was dead or nesting.

Trapping and identification of wild-born nesting females

Trapping of wild-born females was carried during egg collection campaigns in the breeding season of the periods 1997-1998, 2001-2009 and 2015-2016 (see details in online appendix C). Egg collection campaigns aimed at building the founder population of the supportive captive-breeding (Lesobre et al. 2010, Chargé et al. 2014). Females were caught using nylon snares around their nest or around their few days old chicks. In total 143 wild-born females were caught while nesting to be equipped with a transmitter or for transmitter replacement. In addition, 10 wild-born females captured and equipped with VHF/PTT transmitters as juveniles were found nesting in the following years (see Hardouin et al. 2012 for more details of the capture and monitoring procedures).

Data collection

Breeding parameters

Six breeding parameters were assessed from breeding survey data collected from 2002 to 2016: the nesting effort (number of nesting attempts per breeding season per female), the clutch size, the egg volume, the nest initiation date, the daily nest survival rate and the daily brood survival rate. The number of years of survey slightly varied among breeding parameters and is detailed in online appendix D.

- Nest survey

Nests were located from a collaborative survey with shepherds and from individually tracked females. Because of the bias inherent to the trapping and egg collection campaigns (all wild-born non-equipped nesting females had their eggs collected if not hatched and were caught) and to avoid confounding factors between transmitters presence and female origin (wild-born and captive-bred), we only selected, those nests for which the nesting female was equipped with a transmitter at nest initiation. In total, 703 nests from 305 females were selected for this study. For wild-born females, 300 nests were from 91 wild-born females first captured on nest and 21 were from 10 females captured and marked at the juvenile stage. For captive-bred females (n nests = 382), we selected nests from cohorts of females that were released in their first year of life from August to November (in autumn before the breeding season, n nests = 122, n females = 74) and from February to May (in spring during the breeding season, n nests = 260, n females = 130). Nests were visited on average every 6 ± 3.60 days. In addition, since

2013, camera traps were deployed on some of the monitored nests ($n = 45$), providing a continuous survey effort and more accurate assessments of nest fate. Nests equipped with camera traps were visited on average every 8 ± 5.07 days. Nest failure was considered for a visit interval if the clutch disappeared without signs of hatching (Mabee 1997) or was abandoned. We considered a nest to have survived if at least one egg hatched (Mayfield 1975).

The clutch size was defined as the maximum number of eggs observed in the nest. Since 2003, the length, width (to the nearest hundredth of cm) and mass (to the nearest tenth of gram) of each egg were measured. The width and length of eggs were then used to calculate the egg volume (Vol) in cm^3 (see details in Bacon et al. 2017). The nest initiation date was estimated from the calculation of the eggs' incubation stage (in days) at the time of measurement (based on the egg weight loss equation from Hoyt 1979, see details in Bacon et al. 2017).

The nesting effort was calculated as the number of nests initiated per breeding season per female, including females initiating no nest. We selected females that were constantly monitored along the breeding season. Even if all females were fitted with monitoring devices, technical limitations could cause gaps in their monitoring, which could cause the non-detection of nesting attempts. To increase the nesting attempt detectability we only selected females that were fitted with VHF, monitored from February to end of June with at least one individual sighted every two weeks (it resulted in 173 monitoring histories from 141 females from 2002 to 2014).

Trapping of nesting females causes systematic nest abandonment thus, female trapping and egg collection have a positive effect on the nesting effort as they promote replacement clutches. However replacement clutches are initiated later in the breeding season affecting the distribution of nest initiation dates. Therefore, for those two parameters, we excluded females from the years they undergone collection of their eggs (see online appendix D).

- Brood survey

Assessing breeding success after hatching and before fledging in species with nidifugous chicks is difficult. It requires the marking and close monitoring of all individuals, a delicate operation which may affect chick survival at this very sensitive stage of life (Barron et al. 2010). As such, we chose to not mark chicks and rather assess the fate of broods through the

monitoring of brooding females. Therefore, between 2002 and 2014, nesting females fitted with VHF transmitters that brought at least one egg to hatching were then searched at least once a week. Brood failure was considered for a female monitoring interval if the entire brood disappeared before 60 days of age (Hardouin et al. 2012). In total, we monitored 201 broods from 133 females. Few females (n=12) were captured while rearing chicks, at the nest or after leaving the nest, to take measurement or replace the transmitter.

Statistical analyses

Nest and brood survival analyses

We used the logistic exposure approach of Shaffer (2004) to estimate the daily nest survival rate (probability of a living nest to not fail in one day). Egg collections and female trapping, which were oriented preferentially on nests from wild-born females, cause the end of the nest history and conduct to unknown “natural” final fate. In cases they are occasional and representative of the whole population of nests, nests with unknown final fate can be right truncated at the last date they were known active for daily nest survival analysis. In our study, however, the number of clutches collected was relatively important and biased towards wild-born females. Thus, to obtain unbiased comparisons of breeding performances between wild-born and captive-bred females, we excluded nests with unknown final fate from the analysis (following Stephen Dinsmore personal communication and Manolis et al. 2000). Finally, as records of periodic nest visits were standardized from 2003 only, we discarded data prior to 2003.

The same statistical approach was used to study brood survival, at the exception that the exposure period starts at hatching and ends 60 days later for successful broods (mean age at fledging, Hardouin et al. 2012 but see details in Bacon et al. 2017).

Clutch size, egg volume, nest initiation date and nesting effort

The nesting effort was analysed using a generalized linear mixed effects model with a Poisson distribution and a log link function. The clutch size was analysed based on ordinal regression using cumulative linked mixed effects models (CLMMs). Egg volumes and nest initiation dates were analysed using linear mixed effects models (LMMs) fitted by maximum likelihood with a Gaussian distribution and an identity link function.

Origin and age factor

We grouped nests in categories based on female origin (wild-born, captive-bred released in autumn and captive-bred released in spring). In addition we assigned to each nest the age of the nesting female: one year old or two years and older (see online appendix E). For wild-born females, only those captured as juveniles could be aged precisely. A previous study focussing only on released females indicated that one year old females had lower breeding performance than older individuals (Bacon et al. 2017). In addition, the percentage of one year old released females initiating at least one nest is low (8%, ECWP unpublished data). Based on this current knowledge, we assumed that all wild-born females with unknown age were two years old and older at their first identification on a nest.

Adjustment variables

In monitored animals, events such as trapping and marking are stressful and may have some effect on subsequent behavioural and demographic patterns (unusual movements, increased mortality, cessation of breeding) once released (Casas et al. 2015, Ponjoan et al. 2008). For nesting female Houbaras, trapping causes nest abandonment (direct effect) but may also have a carry-over effect on subsequent breeding performances. For females trapped on live chicks, trapping may have a direct effect on brood survival affecting either the female or the chicks. Then, we considered an intra-seasonal carry-over effect of trapping for the following parameters: clutch size, egg volume, daily nest survival and daily brood survival rate, when measured on replacement clutch consecutive to the trapping of the female (carry-over trapping). In addition, specifically for the daily brood survival rate, we considered a direct effect of trapping (direct trapping) on the brood when trapping of the females occurred while rearing chicks. Carry-over trapping and direct trapping effects were implemented as binary adjustment variables. To account for the temporal variation of breeding performances within the breeding season, we included a date covariate (in Julian days, 1st of January = 1, implemented as the nest initiation date for egg volume and clutch size, the median date between two nest visits for the daily nest survival rate, and as the hatching date of the nest for the daily brood survival rate, Grant & Shaffer 2012). Finally, we considered temporal variation of the daily survival rate of the nest and brood by including respectively a binary factor informing if the nest was in laying or incubation stage and a continuous covariate indicating the age of the brood since hatching (Grant & Shaffer 2012).

Multi model inference

For each breeding parameter analysis, covariates were rescaled, centralized and standardized by two times the standard deviation (Gelman 2008), and factors with two levels were transformed in binary dummy variables (0-1).

We examined the relationship between the breeding parameters and their corresponding variables by developing sets of candidate models including all additive combinations, quadratic terms of continuous temporal covariates (date² and brood age²) and the interaction between the age of the nesting female and its origin. We kept the trapping carry-over effect and the direct trapping effect in all candidate models of the concerned breeding parameters, to adjust for potential effects. Additionally, current year, female identity and nest identity nested in female identity (only for egg volume analyses) were incorporated as random intercept effects in all models.

We ranked models using the Akaike Information Criterion corrected for small sample size (AICc). The best model ($\Delta AICc = 0$; Burnham & Anderson 2002), was selected to estimate β coefficients for fixed effects covariates. We assumed significance of β s when their 95% unconditional confidence intervals (95% CIs) did not include zero. All analyses were conducted using R 3.3.3 (R Development Core Team, 2017) and the packages lme4 1.1-12 (Bates et al. 2015), Ordinal 2015.6-28 (Christensen 2015) and nest survival (Herzog 2009).

Normality and homoscedasticity of the random residuals were checked graphically from global models, and no overdispersion (Zuur et al. 2009) was observed for the Poisson distribution model.

Results

We analysed the effects of dependent covariates on 6 breeding parameters based on a common statistical approach. To keep the results presentation clear and straightforward, we directly present the coefficients from the best selected models in Table 1. AICc based model ranking selections, which compiled six tables, can be found in online appendix F. From the best models (Table 1), clutch size and egg volume were significantly declining along the breeding season. Daily nest survival was significantly higher during the nest initiation stage than during the incubation stage, while daily brood survival was increasing with the age of the brood. Carry-over trapping had no significant effects on the breeding parameters tested and direct trapping of females while rearing chicks had a very strong significant negative impact on the daily survival of the brood (Table 1).

Chapitre 2. Evaluation du coût au lâcher dans une population renforcée : une question de stratégie de lâcher

Table 1. Coefficients (\pm 95% CIs) results from variables selected in the best models (Δ AICc=0).

Variables	Nesting effort	Nest date	initiation	Clutch size	Egg volume	DNSR	DBSR
Carry-over trapping	-	-	-	0.09 [-0.44 ; 0.63]	0.00 [-0.99 ; 1.00]	0.07 [-0.35 ; 0.48]	-0.35 [-1.09 ; 0.40]
Direct trapping	-	-	-	-	-	-	-1.83 [-2.73 ; -0.93]
Date	-	-	-	-0.97 [-1.35 ; -0.59]	-1.58 [-2.18 ; -0.98]	Not selected	Not selected
Brood age	-	-	-	-	-	-	0.68 [0.16 ; 1.19]
Nest stage	-	-	-	-	-	-2.52 [-4.49 ; -0.56]	-
Female origin (Intercept = Wild-born):		Not selected	Not selected			Not selected	
Released in autumn	-0.47 [-0.99 ; 0.05]				-0.80 [-2.48 ; 0.89]		0.11 [-0.55 ; 0.76]
Released in spring	-0.64 [-1.16 ; -0.13]				-1.71 [-3.12 ; -0.31]		-0.50 [-1.00 ; 0.00]
Female's age	1.74 [1.10 ; 2.37]	-11.45 [-17.87 ; -5.03]		1.01 [0.47 ; 1.55]	4.13 [2.74 ; 5.51]	Not selected	1.05 [0.41 ; 1.68]

“Not selected” indicates that the covariate was not selected in the best set of models and “-” indicates that the covariate was not included in the global model. DNSR = Daily Nest Survival Rate, DBSR = Daily Brood Survival Rate. For binary factor Carry-over trapping : Not consecutive to trapping = 0, Carry-over trapping = 1. For binary factor Direct trapping: No trapping = 0, Trapping of brooding female = 1. For binary factor Nest stage: Laying stage = 0, Incubation stage = 1. For binary factor Female's age: One year old females = 0, Two years and older females = 1. Coefficients are in bold, where 95% CIs do not include zero.

Age effect was selected in all models at the exception of the daily nest survival rate. When selected, age differences were significant with lower breeding performances of one year old females (Table 1).

The origin factor was selected in the best model set for nesting effort, egg volume and daily brood survival rate. In Table 1, for the female origin factor, the results show the differences with respect to a reference level in intercept. We defined wild-born females as the reference level in Table 1 but all levels of the female origin factor were set as the reference level at the intercept to assess potential significant differences. Captive-bred females were initiating fewer nests and laying smaller eggs than wild-born females (Figs 2A, B). However, these effects were significant only for captive-bred females released in spring relative to wild-born females (Table 1). Captive-bred females released in autumn had intermediate values of nesting effort and egg volume, but non-significantly different from the two other groups (Table 1). Finally, captive-bred females released in spring had lower daily brood survival than wild-born females and captive-bred females released in autumn (Fig 2C, Table 1), and the difference between captive-bred females released in spring and wild-born females was marginally significant (Table 1).

None of the best models included the interaction between age of the nesting female and its origin.

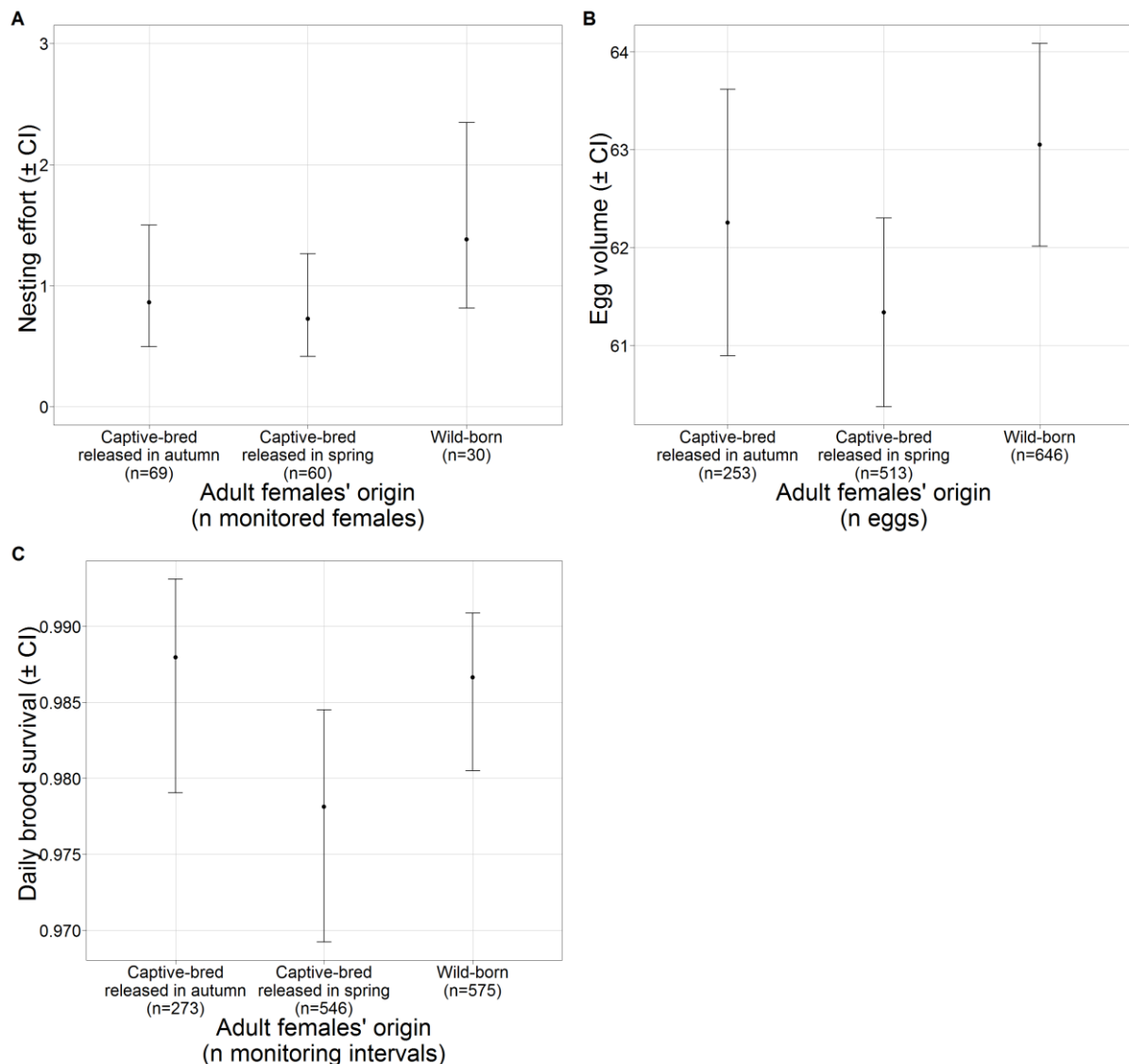


Figure 2. Prediction of (A) the nesting effort, (B) egg volume and (C) daily brood survival as a function of the origin of the female

Discussion

The assessment of the breeding performances of released individuals is of main importance in translocation programmes (Bertolero et al. 2009). Within this study, we investigated the cost of release through the comparison with breeding parameters of wild females and revealed how the release strategy may influence the magnitude of this cost. This is a prerequisite to adapt and improve translocation strategies and consecutively increase the chance of translocation success (Armstrong et al. 2007).

Most breeding parameters (except nest survival) consistently showed age-specific variation suggesting an increase of breeding performances between one year old and older females, in agreement with previous study (Bacon et al. 2017). As individual heterogeneity was taken into account in our statistical framework (see Nussey et al. 2006, van de Pol & Verhulst 2006), the observed age effects may be explained by longitudinal improvement of individuals, i.e., gain of breeding experience or increase in breeding investment (Curio 1983), rather than by population processes (e.g., selection of the best individuals through time). The lack of age variations on the daily nest survival may be explained by the weight of external factors, such as environmental conditions (Morales *et al.* 2002) or predation which is a prominent cause of nest failure in birds (Martin 1995), including Houbaras (Bacon et al. 2017, Koshkin et al. 2016), potentially overriding any age dependent effects.

Regardless of age effects, our results indicate that, for some of the breeding parameters studied, wild-born individuals performed slightly (not significantly) better than individuals translocated in autumn and significantly better than individuals translocated in spring. More precisely, wild-born females were initiating more nests with larger eggs relative to captive-bred females released in spring. In addition, the daily brood survival of captive-bred females released in spring was lower than for wild-born females. This cost of release has a marked size effect. It corresponds to a ~47% decline in nesting effort and a ~40% decline in brood survival (from hatching to fledging) when considering adult females released in spring relative to adult wild-born females (Figs 2A, C).

Conversely to our expectations, we did not observe any interaction between the age of the female and its origin. This result is consistent with the long term (i.e., permanent) release cost on breeding parameters observed in other translocated species (see e.g., Sarrazin et al. 1996). It is also consistent with previous findings in Houbaras that released captive-bred females exhibit age dependent patterns of variation in breeding performances similar to those observed in many vertebrate populations in the wild (i.e., a bell shape trend divided in youth, adulthood and senescent ages, see discussion in Bacon et al. 2017).

As differences between wild-born and captive-bred individuals persisted in the long-term, we cannot exclude that genetic causes related to captive-breeding issues partly explain the cost of release. However, strong and restrictive guidelines are conducted in the ECWP captive breeding programme (Chargé et al. 2014). They aim to minimize the loss of genetic variation and adaptation to captivity in the captive population to maximize the fitness of individuals

released into the wild, while reducing the genetic consequences of the reinforcement programme on wild populations (Chargé et al. 2014). Nevertheless, the relaxation of sexual and natural selection and adaptation to captivity may explain part of the lower breeding performances of captive-bred individuals in the wild (Araki et al. 2007, Frankham 2008). Beside, owing to the strong translocation effort (see online appendix B), a substantial proportion of wild-born individuals may be offspring from translocated birds (see general discussion in Barbanera et al. 2010), which may explain that breeding performances of released and wild-born females are relatively close. Therefore, it is likely that most differences among the two groups are related to non-genetic issues.

At the phenotypic level, previous works on captive breeding/rearing in birds have suggested that demographic differences between released and wild-born individuals can be explained by the lack of exposure to adult behaviour of chicks hand-reared in captivity (Roche et al. 2008), permanently lowering their fitness in the wild (Buner & Schaub 2008, Buner et al. 2011, Pérez et al. 2015, Sánchez-García et al. 2011). Although wild-born and released captive-bred Houbara females have a similar diet (Bourass & Hingrat 2015) and exploit equivalent ecological niches (Monnet et al. 2015), released females may be less efficient in finding and exploiting resources (Champagnon et al. 2012). This could explain the lower investment of captive-bred females in reproduction (e.g. egg production), which may consecutively impact the survival of the chicks. In species with precocial chicks (including nidifugous chicks), smaller eggs contain generally less yolk giving rise to chicks in lower conditions with lower nutrient reserves at hatching and more prone to early mortality (Amundsen & Stokland 1990, Blomqvist et al. 1997, Galbraith 1988, Williams 1994).

Our results indicate that the release cost varies according to the period of release (autumn versus spring). Although differences were non-significant, captive-bred females released in autumn had consistently higher nesting effort, egg volume and daily brood survival values than females released in spring (Table 1). Assuming that survival and reproductive parameters positively covary (e.g., "fixed heterogeneity", Cam et al., 2016), such pattern may be related to the death of the less performant females between their release and the breeding seasons among females released in autumn. This hypothesis is supported by previous findings showing that harsh environmental conditions in autumn and winter are significantly lowering post release survival rates compared to spring releases (Hardouin et al. 2014), representing a stronger environmental filter affecting primarily weak individuals.

It is important to notice that not all breeding parameters differed between wild-born and captive-bred females. The origin of females was not selected in the best model for clutch size, nest initiation date and daily nest survival analysis. Similar heterogeneous responses of multiple breeding parameters to female origin was observed by Hill & Roberston (1988) on a reinforced ring-necked pheasant (*Phasianus colchicus*) population, where wild-born and captive-bred released females had similar nesting effort and nesting success, yet chick survival to fledging and total productivity was higher for wild-born females.

Management implications

We observed consistent permanent reductions of some breeding parameters of captive-bred released females relative to wild-born females. The magnitude of these differences points up the necessity to assess demographic costs in translocated populations. The cost of release, as we named it, appears to be dependent on the translocation strategy (period of release), which implies that it could be buffered by adapting translocation strategies (favouring autumn releases). Yet, the current strategy (spring and autumn releases) seems suitable regarding the multiple objectives of the reinforcement programme, i.e., reinforcement of the wild population and supplementation for hunting (falconry). For autumn releases, environmental stochasticity may select individuals in good conditions (Hardouin et al. 2014) that will later breed with relatively higher parameters (as suggested by the present results). On the other hand, whether outcomes from spring releases will be less certain in terms of breeding performances, higher survival rates at this season will help maintaining the population size to a level that can sustain hunting pressure (Hardouin et al. 2014). Finally, although differences were observed between wild-born and captive-bred females, our results confirm the capacity of captive-bred females to reproduce in the wild and to contribute to the dynamics of the population beyond their individual history. This partially supports the success of the reinforcement programme (Bertolero & Oro 2009) and provides strong basis for more integrative and quantitative success assessment (Robert et al. 2015a).

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Supplementary materials – Article 2

Appendix A. Breeding stations of the Emirates center for Wildlife Propagation (ECWP)

ECWP is organized into a network of specialized stations: two breeding stations and four rearing stations where future releases are prepared for reinforcement. The two breeding stations, Missouri station created in 1995 and Enjil Station created in 2005, respectively hold 3 500 and 6 000 breeders, all kept in individual cages. All eggs produced through the artificial reproduction process are incubated at Missouri station in an incubation building of a full capacity of 40 000 eggs. The annual production capacity is 20 000 birds and all stations together can shelter 30 000 birds (breeders and production).

Appendix B. Number of captive-bred Houbaras released per year in the Eastern intervention area of the ECWP

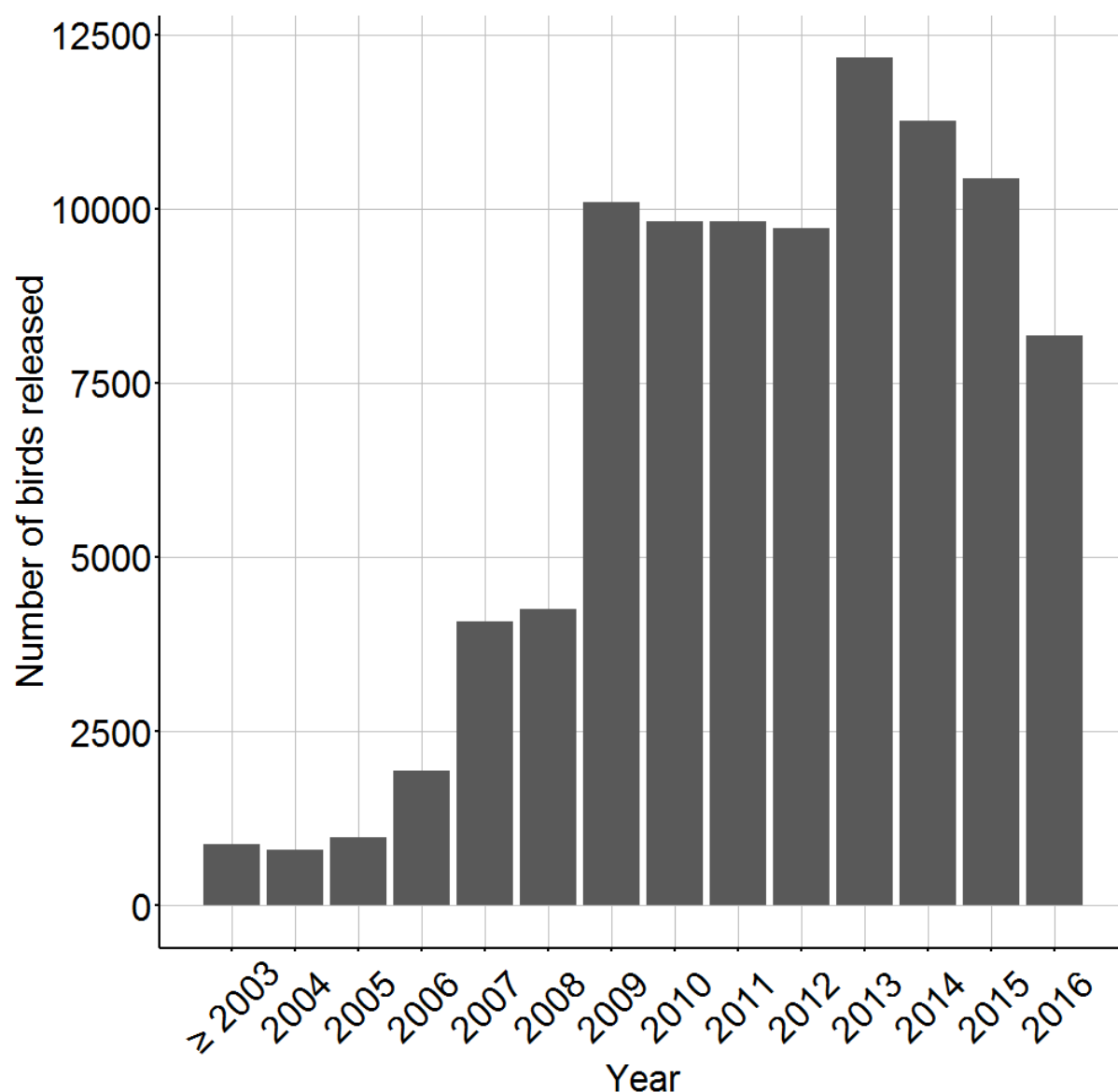


Figure B. Number of captive-bred Houbaras released per year in the Eastern intervention area of the ECWP

Appendix C. Trapping and identification of wild-born nesting females

Trapping of wild-born females were carried during the breeding periods in 1997-1998, 2001-2009 and 2015-2016. Females were caught using nylon snares around their nest or around their few days old chicks (Launay et al., 1999, Seddon et al., 1999). Once caught, females were identified as wild-born if they were not marked as captive-bred individuals (ring or PIT-tag identification). Birds were then banded with a unique metal band and fitted with a transmitter (VHF, satellite or GSM). Trapping was conducted during egg collection campaigns that aimed at building the founder population of the supportive captive-breeding

(Chargé *et al.* 2014, Lesobre *et al.* 2010). It means that all nests from wild-born females where trapping occurred had their eggs collected (the whole clutch), as well as a part of their replacement clutch and clutch from the consecutive years when they were monitored. In total 143 wild-born nesting females were caught and 177 of their clutches were collected. In addition, 40 captive-bred females were caught at the nests to be equipped with a transmitter or for transmitter replacement. Consequently, their eggs were also collected (40 nests). Finally, 10 wild-born females captured and equipped with VHF/PTT transmitters as juveniles (see Hardouin *et al.* 2012 for more details of the capture and monitoring procedures) were found nesting in the following years.

Appendix D. Sample size differences for breeding parameters related to the nest.

The sample sizes of the datasets varied among breeding parameters related to the nests. Explanations and justifications are provided below.

Overall, from 2002 to 2016, 703 nests from 305 females were selected for this study and these 703 nests were used for clutch size analysis.

From the clutch size dataset, egg volume data were not available for 114 nests, because no or wrong measurements were made. Egg volume analyses were conducted from 2003 to 2016.

For daily nest survival rate, 532 nests from 2003 to 2016 were implemented in the analysis. As records of periodic nest visits started in 2003, we did not include the year 2002 in the daily nest survival analysis. We excluded nests with unknown final fate ($n=105$, because of the female trapping protocol) and nests with no or uncertain visit records as they cannot be included in our survival models based on time exposure ($n=66$).

Trapping of nesting females causes systematic nest abandonment thus, female trapping and egg collection have a positive effect on the nesting effort as they promote replacement clutches. However replacement clutches are initiated later in the breeding season affecting the distribution of nest initiation dates. Therefore, for those two parameters, we excluded females from the years they undergone collection of their eggs. Finally, 399 nests, from 2003 to 2016 were used for the nest initiation date analysis and 159 monitoring histories from 132 females from 2002 to 2014 for nesting effort analysis.

Appendix E. Age distribution of nesting females per year and origin

Chapitre 2. Evaluation du coût au lâcher dans une population renforcée : une question de stratégie de lâcher

Table E. Number of nests in function of females's origin, age and year

Origin of nesting females	Age	Year														
		2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Wild-born	1	0	0	0	0	0	1	2	1	2	0	0	0	0	1	0
	≥2	24	42	56	11	34	49	38	29	10	1	1	0	0	9	10
Captive-bred released in spring	1	10	0	0	0	8	1	0	2	0	3	1	3	0	5	0
	≥2	0	9	29	10	20	29	51	5	17	2	11	7	6	13	18
Captive-bred released in autumn	1	0	1	15	0	7	4	0	1	0	0	4	5	1	0	3
	≥2	0	0	8	1	9	8	10	2	6	5	7	4	1	12	8

Appendix F. AICc model selection – First five models based on AICc ranking

Table F.1. AICc model ranking of the first five models for nesting effort analyses

Models	logLik	AICc	ΔAICc	AICcw
Origin + Age	-132.74	278.00	0.00	0.60
Origin	-135.95	280.10	2.11	0.21
Origin + Age + Origin x Age	-131.70	280.40	2.32	0.19
Age	-151.11	312.60	34.57	0.00
Null	-158.02	322.20	44.16	0.00

Table F.2. AICc model ranking of the first five models for nest initiation date analyses

Models	logLik	AICc	ΔAICc	AICcw
Age	-1587.21	3184.60	0.00	0.63
Age + Origin	-1586.13	3186.60	1.99	0.23
Age + Origin + Origin x Age	-1584.58	3187.70	3.08	0.13
Origin	-1590.82	3193.90	9.27	0.01
Null	-1593.15	3194.40	9.81	0.01

Table F.3. AICc model ranking of the first five models for clutch size analyses

Models	logLik	AICc	ΔAICc	AICcw
Age + Carry-over trapping + Date	-605.97	1228.1	0	0.378
Age + Carry-over trapping + Date + Date ²	-605.99	1228.2	0.11	0.358
Age + Carry-over trapping + Date + Origin	-605.45	1231.2	3.08	0.081
Age + Carry-over trapping + Date + Date ² + Origin	-605.47	1231.2	3.18	0.077
Age + Carry-over trapping + Date + Origin + Origin x Age	-603.66	1231.8	3.63	0.062

Chapitre 2. Evaluation du coût au lâcher dans une population renforcée : une question de stratégie de lâcher

Table F.4. AICc model ranking of the first five models for egg volume analyses

Models	logLik	AICc	Δ AICc	AICcw
Age + Carry-over trapping + Date + Origin	-3939.26	7898.7	0	0.329
Age + Carry-over trapping + Date + Origin + Origin x Age	-3937.51	7899.2	0.55	0.25
Age + Carry-over trapping + Date	-3942.11	7900.3	1.63	0.145
Age + Carry-over trapping + Date + Date ² + Origin	-3939.24	7900.7	1.98	0.122
Age + Carry-over trapping + Date + Date ² + Origin + Origin x Age	-3937.41	7901.1	2.41	0.099

Table F.5. AICc model ranking of the first five models for daily nest survival rate analyses

Models	logLik	AICc	Δ AICc	AICcw
Carry-over trapping + Nest stage	-643.23	1296.5	0	0.267
Carry-over trapping + Nest stage + Date	-642.46	1297	0.47	0.211
Carry-over trapping + Nest stage + Age	-643.11	1298.3	1.77	0.11
Carry-over trapping + Nest stage + Date + Date ²	-642.25	1298.6	2.07	0.095
Carry-over trapping + Nest stage + Age + Date	-642.41	1298.9	2.4	0.08

Table F.6. AICc model ranking of the first five models for daily brood survival rate analyses

Models	logLik	AICc	Δ AICc	AICcw
Age + Direct trapping + Carry-over trapping + Origin + Brood age	-361.22	740.6	0	0.128
Age + Direct trapping + Carry-over trapping + Origin + Brood age + Date	-360.21	740.6	0.02	0.127
Age + Direct trapping + Carry-over trapping + Origin + Brood age + Date + Date ²	-359.36	740.9	0.34	0.108
Age + Direct trapping + Carry-over trapping + Brood age + Date	-362.89	741.9	1.32	0.066
Age + Direct trapping + Carry-over trapping + Brood age	-363.97	742	1.45	0.062

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Chapitre 2. Evaluation du coût au lâcher dans une population renforcée : une question de stratégie de lâcher

Chapitre 3. Qualité d'habitat et démographie : une relation temporelle

Résumé

L'indice de qualité d'habitat issu des modèles de niche, qui reflète une variabilité spatiale de l'occurrence d'une espèce, a fréquemment montré des liens contrastés avec les performances démographiques locales (survie, productivité) chez de nombreuses espèces (relation positive, négative ou nulle). Une explication serait que le lien entre indice de qualité d'habitat et démographie est influencé par des processus densité-dépendants et temporels. En nous appuyant sur le suivi de plus de 3000 nids de l'outarde Houbara nord-africaine sur 12 années, nous avons examiné si l'indice de qualité d'habitat modélisé sur l'aire de reproduction de l'espèce est relié à la survie des nids le long de la saison de reproduction et en prenant en compte les variations de conditions météorologiques. Nous avons observé que le lien entre indice de qualité d'habitat et survie des nids change progressivement au long de la saison de reproduction, et que cette variation intra-annuelle est consistante entre les années. Nos résultats supportent l'hypothèse qu'il existe des variations de l'utilisation de l'habitat au niveau intra-annuelle et que des interactions biotiques influencent le lien entre indice de qualité d'habitat et démographie tout au long de la saison de reproduction. Malgré sa complexité, l'utilisation statique de l'indice de qualité d'habitat ne semble pas refléter la complexité des modèles démographiques et leur dynamique intra-saisonnière, et l'utiliser comme simple proxy de la démographie pourrait entraîner des erreurs d'inférence.

Mots-clés : Dynamique saisonnière, interactions biotiques, modèles de niche, survie des nids

Article 3. Habitat suitability and demography: a time dependent relationship

Bacon Léo, Hingrat Yves, Monnet Anne-Christine, Jiguet Frédéric, Sarrazin François, Robert Alexandre

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Habitat suitability and demography, a time-dependent relationship

Léo Bacon^{1,2}  | Yves Hingrat^{1,3} | Frédéric Jiguet² | Anne-Christine Monnet^{1,2} | François Sarrazin² | Alexandre Robert²

¹Emirates Center for Wildlife Propagation, Missouri, Morocco

²Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Museum National d'Histoire Naturelle, Paris, France

³RENECO International Wildlife Consultants LLC, Abu Dhabi, UAE

Correspondence

Léo Bacon, Emirates Center for Wildlife Propagation, Missouri, Morocco.
Email: bacon.leo@gmail.com

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Abstract

The habitat suitability index, which reflects spatial variability in species occurrence probability, has been shown to exhibit various contrasting relationships with local demographic performances (survival, productivity) in several species. One proposed explanation for these discrepancies is that the link between the habitat suitability index and demography is influenced by density-dependent, temporally variable processes. Based on the survival rates of more than 3,000 nests monitored over 12 years in the North African Houbara Bustard, we investigated whether the habitat suitability index computed over the species breeding range is related to nest survival throughout the breeding season, accounting for variation in meteorological conditions. We found that the relationship between the habitat suitability index and nest survival progressively changes along the breeding season and that this intra-annual variation is consistent between years. Our results support the hypothesis that variation in space use occurs intra-annually and that biotic interactions throughout the breeding season strongly influence the habitat suitability index–demography relationship.

KEYWORDS

Biotic interactions, nest survival, niche modeling, niche switch, seasonal dynamics

1 | INTRODUCTION

The habitat suitability index (HSI) is a probability of species presence inferred from ecological niche modeling, by relating the occurrence of a species at a given location to environmental features (Guisan & Thuiller, 2005). The output of species distribution models based on such niche modeling is considered as a measure of the suitability of environmental features for the occurrence of the target species (VanDerWal et al., 2009). Thus, if habitat selection is adaptive, habitat attractiveness should match demographic performance (Battin, 2004; Hutchinson, 1957) and the HSI should be related not only to the probability of occurrence, but also to other key parameters of populations.

Recent studies have attempted to link the HSI to various demographic parameters, such as survival (Monnet, Hardouin, Robert,

Hingrat, & Jiguet, 2015; Unglaub, Steinfartz, Drechsler, & Schmidt, 2015) and reproductive parameters (Brambilla & Ficetola, 2012; Pellissier et al., 2013; Thuiller et al., 2014; Unglaub et al., 2015). Results from these studies exhibited various contrasting relationships, including positive, negative, and null correlations. Three general explanations have been used to rationalize these complex and inconsistent relationships. First, some empirical evidence suggests that environmental conditions favoring both species presence and the demographic performance of that given species can be distinct from those favoring only its presence (see an example in an alien population in Ficetola, Miaud, Pompanon, & Taberlet, 2008). For example, ecological theory regarding source–sink dynamics (Pulliam & Danielson, 1991) and ecological traps (Kristan, 2003) indicates that, in certain species, some individuals may be located outside the bounds of the

species niche (Bateman, VanDerWal, & Johnson, 2012; Schurr et al., 2012; Titeux, Dufrene, Radoux, Hirzel, & Defourny, 2007). Second, high HSI values might reflect high local densities (Tôrres et al., 2012), and various ecological processes can be modulated by density (Oliver et al., 2012), such as intra- and interspecific competitions or predation (Fernández-Bellon, Cortés-Avizanda, Arenas, & Donàzar, 2016; Guisan & Thuiller, 2005; Gunnarsson & Elmer, 2008; Thuiller et al., 2014), which can in turn produce unexpected and complex relationships between the HSI and demographic rates. A third proposed explanation is that the link between the HSI and demography is temporally variable (Wiszniewski et al., 2013). More specifically, the influence or correlation between some environmental features and demographic rates can vary within and between years due to factors such as the phenology of the species, seasonal and interannual variations in biotic interactions, demographic heterogeneity, meteorological fluctuations, or climate change (Yang & Rudolf, 2010). For example, many studies have documented that biotic interactions are not static (Brooker, 2006; Callaway et al., 2002; Forchhammer, Post, Berg, Høye, & Schmidt, 2005; Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010), and static species distribution models may fail to recognize the effects of species interactions if temporal variation is not considered (see Bateman et al., 2012). Other results indicate that this is also true for abiotic factors, such as short-term meteorological variation (Reside, VanDerWal, Kutt, & Perkins, 2010). Finally, the link between the HSI and demography can change, for example, at the intra-annual scale, through niche dynamic processes, for example, a switch of the niche (i.e., space use) between the breeding and nonbreeding seasons in species with seasonal breeding behaviors (Hayes, Cryan, & Wunder, 2015; Nakazawa, Peterson, Martinez-Meyer, & Navarro-Siguenza, 2004; Yannic et al., 2014). Any subsequent change in local population size or density can in turn impact demographic rates (Brook & Bradshaw, 2006; Fernández-Bellon et al., 2016; Frederiksen & Bregnballe, 2000).

Here, we aim to examine the relationship between the HSI and demography at both interannual and intra-annual scales, with special emphasis on the dynamic aspect of this relationship. Using data collected from a longitudinal nest survey in a bird species, the North African Houbara Bustard (*Chlamydotis undulata undulata*) (hereafter "Houbara"), we explored whether the breeding performance (estimated by the daily nest survival rate) is related to the HSI computed from independent data, which represents a suitability index of presence, over the breeding range of the species and over several years, depending on meteorological conditions, as well as throughout the breeding season.

Previous research on Houbara and its breeding environment indicates that (1) there are significant biotic and abiotic changes in the breeding environment of birds along the breeding season (ranging from February to June), including meteorological changes (Warner, 2004) and changes in intraspecific interactions (Hingrat, Saint Jalme, Ysnel, Le Nuz, & Lacroix, 2007), as well as in interspecific interactions (Bourass et al., 2012; Hingrat, Ysnel et al. 2007); (2) young, inexperienced females tend to breed later in the season compared to older females (Bacon, 2013), which is likely to generate some demographic heterogeneity along the season; (3) interannual variation in meteorological

conditions can affect demographic rates (see Hardouin et al., 2014 for survival); (4) in captive-bred individuals released in the wild, survival is related to changes in local HSI values along postrelease movements (Monnet et al., 2015). Birds moving to sites with lower HSI values than the HSI values of their release site have a reduced survival probability, while individuals moving to sites with higher HSI have increased survival probability. However, individuals with the highest HSI gain do not have the highest survival probability. Monnet et al., 2015 set forward the hypothesis that higher densities in high HSI sites may enhance deleterious ecological processes such as intraspecific competition.

Based on these elements, we expect a negative relationship between the HSI of the Houbara breeding range and the daily nest survival rate, potentially caused by density-dependent effects that could be magnified in years with low resource availability (e.g., low precipitation) or during the peak of the breeding season (in April) when breeding activity and competition are the highest.

2 | METHODS

2.1 | Study species and study areas

The Houbara is a medium-sized, nonmigratory bustard inhabiting semidesert habitats from North Mauritania to Egypt. It is a ground-nesting, gyneparental incubating species which breeds from mid-February to mid-June. Females typically lay 2–3 eggs per clutch, which they incubate for about 23 days (Gaucher, 1995). Houbara chicks are nidifugous.

Our study was conducted between 2003 and 2014 in two study areas in southern and eastern Morocco totaling 75,000 km² (Figure 1). These two study areas are part of the Emirates Center for Wildlife Propagation (ECWP) intervention areas. In these intervention areas, the Houbara population is reinforced through regular releases of captive-bred individuals (Chargé et al., 2014; Hardouin et al., 2014).

2.2 | Data collection

2.2.1 | Demographic data

Between 2003 and 2014, 3,108 nests were located from a collaborative survey involving local shepherds and from the monitoring of females fitted with radio and satellite transmitters (see Appendix A1, Table A1.1, Figure A1.1 in Appendix S1). For most nests, visits occurred every 1–10 days (first and ninth centile of visit interval distribution). Visits were more frequent at the end of the incubation stage to obtain better accuracy on the dates of hatching. In addition, in 2013 and 2014, camera traps were deployed on some of the monitored nests ($n = 231$), to obtain a continuous survey effort at these nests. Nests equipped with camera traps were visited every 3.7–8 days (first and ninth centile of visit intervals distribution, see Appendix A1, Table A1.2, Figure A1.2 in Appendix S1). Nest monitoring effort was constant between years (see details in Appendix A1 in Appendix S1). Nest failure was considered to have occurred for a given visit interval if the clutch disappeared without signs of hatching (Mabee, 1997) or was abandoned.

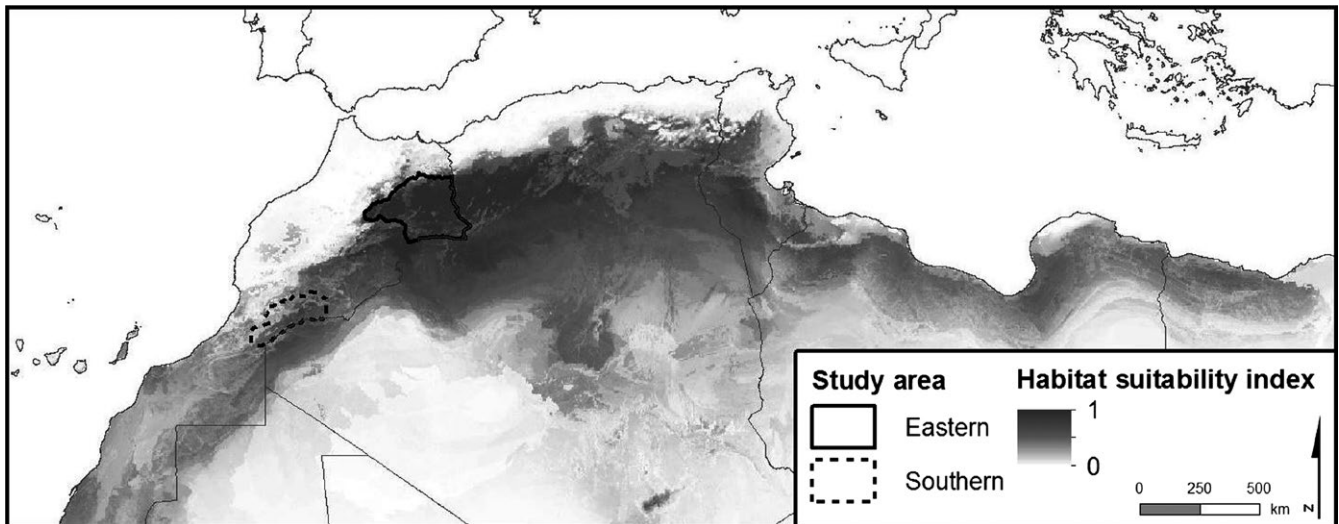


FIGURE 1 Locations of the study areas within the habitat suitability index (HSI) gradient of the North African Houbara Bustard (*Chlamydotis undulata undulata*) breeding range (Monnet et al., 2015)

2.2.2 | Spatial covariate: the HSI

We extracted the value of the habitat suitability index (HSI) of the Houbara breeding range, computed by Monnet et al. (2015) (Figure 1), at each nest location. This index is based on occurrences (presence and pseudo-absence) related to spatial variation in the environment, including both land cover and climate variables (see Appendix A2 in Appendix S1). Considering the large decline of the species these last decades, Monnet et al. (2015) used both historical and recent occurrence data to model the ecological niche of Houbara. Historical data were randomly sampled in the historical breeding range of the species (Goriup, 1997) and completed by data collected in Morocco, Tunisia, and Algeria between 1997 and 2012 from monitoring wild adult birds with satellite and VHF transmitters recorded during the breeding period (from February to May, see Monnet et al., 2015 for more details). Monnet et al. (2015) summarized occurrence and environmental data at a 2.5 arc-minutes grid (approximately 4.5×4.5 km). They performed a consensus approach using the BIOMOD computer platform (Thuiller, Lafourcad, Engler, & Araujo, 2009). All models were evaluated by computing the area under the curve (AUC) and showed high predictive performance (AUC > 0.85, Araujo, Pearson, Thuiller, & Erhard, 2005). Following one of the best consensus methods identified by Marmion, Parviainen, Luoto, Heikkinen, and Thuiller (2009), the final HSI was obtained by calculating the mean value of the predictions across the runs of seven modeling techniques. Further details on occurrence data and niche modeling techniques can be found in Ref. Monnet et al. (2015).

2.2.3 | Temporal covariates

In semidesert habitats, meteorological conditions from past seasons have a major influence on seasonal productivity of the habitat (e.g., precipitation legacies; Ozenda, 2004; Reichmann, Sala, & Peters, 2013; Sala, Gherardi, Reichmann, Jobbágy, & Peters, 2012) and potentially

habitat selection within Houbara populations. Therefore, variability in meteorological conditions before the breeding season may affect the relevance of the static HSI during breeding seasons. We thus assigned for all nests from the same study area the average precipitation value (*Prec*, in mm/hr) and average surface air temperature value (*Temp*, in °C) from the previous year, obtained from the Global Land Data Assimilation System (GLDAS v001, Rodell et al., 2004).

To account for potential variation in the daily nest survival rate within the nesting season, we included the date in the nesting season (*Date*, as julian days) as an intraseasonal explanatory covariate, as it may represent a gradient of meteorological conditions (Warner, 2004), habitat selection (Hingrat, Saint Jalme et al. 2007), and species interaction (Hingrat, Ysnel et al. 2007) within the breeding season.

All covariates were rescaled, being centralized and standardized by two times the standard deviation (Gelman, 2008). Because our main objective was to assess the relationship between daily nest survival rate and HSI (i.e., a spatial index of quality, which already carries information on average local climatic conditions), the rescaling of meteorological data (meteorological anomalies) was done independently for the two study areas, which allowed us to increase their interannual variation at the expense of the spatial variation. Thus, our data allowed us to assess the combined effects of spatial (HSI: one unique value for each nest location over the study period) and temporal (meteorological anomalies, date within the breeding season) variations on demography. Correlations between the rescaled covariates were all weak (Pearson correlation tests $|r| < 0.3$).

2.3 | Nest survival and statistical analysis

We assessed the effects of spatial and temporal covariates on the daily nest survival rate (probability of a live nest to not fail in 1 day), using the logistic exposure approach from Shaffer (2004). This generalized linear method incorporates a logit link function that performs with various exposure periods between nest visits (Shaffer,

TABLE 1 Model-averaged coefficients and 95% confidence intervals (CIs) from the set of best models ($\Delta\text{AICc} < 2$) for the analysis of the additive effects of spatial and temporal covariates on the daily nest survival rate

Covariate	Coefficients	Lower CI	Upper CI	Relative importance
Date	-0.38	-0.49	-0.27	1
HSI	-0.11	-0.22	0.01	0.69
Prec	0.09	-0.02	0.21	0.52
Temp	-0.03	-0.13	0.07	0.28

The relative importance of the covariate is the sum of AICc weights of the models where the covariate occurs. Random effects for the year and study area are fitted for all models. Coefficients are in bold where CIs do not include zero.

2004). It attempts to overcome biases associated with other estimator techniques that capture apparent nest survival (proportion of nests with at least one egg hatching). For hatching nests, the exposure period stops with the first egg hatching. This approach does not require the exact day of nest failure but the interval within which the failure occurred. We focused on the daily survival rate as we considered it to be the most relevant proxy of breeding performance to link to large-scale environmental features. The Houbara has nidifugous chicks, and data on chick survival or total reproductive output are scarce. In addition, nests are fixed entities and the link between HSI and nest survival cannot be mitigated by individual movements of chicks. Therefore, we preferred to focus on an easily acquired breeding parameter from which we could have the highest range of HSI sites.

We first examined the relationship between the daily nest survival rate and covariates by developing a set of candidate models including all combinations of additive effects. This first round of model selection allowed us to assess the global relationship between the daily nest survival rate and the HSI while controlling for other potential effects, but intentionally neglecting potential temporal variation in the daily nest survival rate–HSI relationship. As a second step, we specifically investigated whether the daily nest survival rate–HSI relationship could temporally vary within the breeding season and/or be driven by meteorological variation among years by developing a set of candidate models including additive effects and the first order interactions $HSI \times Date$, $HSI \times Prec$, and $HSI \times Temp$. We partitioned our analysis into two separate steps (additive effects only and additive plus interaction effects) because the use of model averaging techniques to compare additive effects is irrelevant when interaction terms are present. The year and study area were incorporated as random effects in all models. We performed a full multimodel inference analysis (Burnham

& Anderson, 2002) in each of these two steps (only the starting full model differed between the two steps).

We ranked models using the Akaike information criterion corrected for small sample size (AICc). For each step, we estimated robust model-averaged coefficients (β) from the set of best models ($\Delta\text{AICc} < 2$; Burnham & Anderson, 2002), based on their AICc weights (the relative likelihood of candidate models based on their ΔAICc). We assumed significance of β for the covariates if their 95% unconditional confidence intervals (CIs) did not include zero. All analyses were conducted using R 3.0.2 (R Development Core Team, 2013) and the packages lme4 1.1.7 (Bates, Martin, Bolker, & Walker, 2015) and MuMIn 1.13.4 (Barton, 2015). The logistic exposure link function implemented in generalized linear mixed models was obtained from the R package nest survival (Herzog, 2009).

3 | RESULTS

From the sample of 3,108 monitored nests, a total of 1,391 (45%) failed. The values of the habitat suitability index (HSI) at the nest locations ranged from 0.10 to 0.91, with a median at 0.86 (see Appendix B1 in Appendix S2).

From the first set of models (focusing on additive effects, see details on model ranking in Appendix B2.1 in Appendix S2), the analysis indicated that the daily nest survival rate decreased with the progression of the breeding season, but no global effect of the HSI on nest survival was observed (Table 1).

The second set of models (models with interactions, see details in Appendix B2.2 in Appendix S2) revealed a strong positive interaction between HSI and $Date$ (Table 2). The daily nest survival rate was negatively related to the HSI early in the nesting season, and this

TABLE 2 Model-averaged coefficients and 95% confidence intervals (CIs) from the set of best models ($\Delta\text{AICc} < 2$) for the analysis of habitat suitability interactions on the daily nest survival rate

Covariate	Coefficients	Lower CI	Upper CI	Relative importance
Date	-0.35	-0.46	-0.23	1
HSI	-0.18	-0.30	-0.05	0.98
Date \times HSI	0.34	0.10	0.58	0.93
Prec	0.11	-0.01	0.22	0.65
Temp	-0.03	-0.13	0.08	0.36
Prec \times HSI	-0.05	-0.29	0.19	0.18

The relative importance of the covariate is the sum of AICc weights for the models where the covariate occurs. Random effects for the year and study area are fitted for all models. Coefficients are in bold where CIs do not include zero.

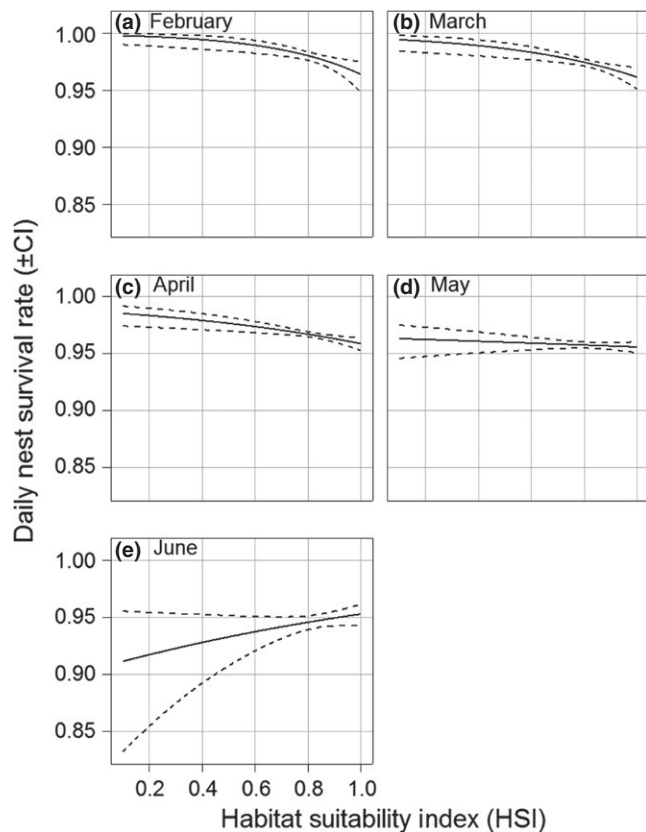


FIGURE 2 Relationship between the daily nest survival rate ($\pm 95\%$ CI) and the habitat suitability index (HSI) for each month of the breeding season. (a) February, (b) March, (c) April, (d) May, and (e) June

relationship became positive by the end of the season (Figure 2). No significant interactions between HSI and meteorological anomalies were found.

To examine whether the $HSI \times Date$ interaction was consistent between years, we developed the full set of candidate models from a global model including the $HSI \times Date \times Year$ interaction, with *Year* implemented as a factor and the study area as a random effects variable. Neither models including the interaction $HSI \times Date \times Year$ ($\Delta AICc = 31.75$) nor $HSI \times Year$ ($\Delta AICc \geq 14.48$) were retained relative to the best models ($\Delta AICc < 2$). Graphical analyses confirmed that the $HSI \times Date$ interaction was very consistent among years (see online Appendix B3 in Appendix S2).

4 | DISCUSSION

From an eco-evolutionary perspective, habitat suitability index (HSI) and demography have strong conceptual links because (1) for a given species, from an evolutionary viewpoint, it is expected that habitat attractiveness will match demographic performance (Battin, 2004; Brambilla & Ficetola, 2012; Hildén, 1965; Losier et al., 2015) and (2) although there are many ecological processes that can influence species' range patterns and dynamics (Thuiller et al., 2008), these

processes affect range dynamics through their effect on demography (reproduction, survival, and dispersal, Cabral & Schurr, 2010; Holt & Keitt, 2005).

However, recent studies indicate that relationships between HSI and demographic components are not always positive (Monnet et al., 2015; Pellissier et al., 2013; Thuiller, Albert, Dubuis, Randin, & Guisan, 2010). This suggests that the ecological processes governing relationships between population demography and a species' environment may be too complex to be integrated into niche modeling. In parallel, it has also been recently demonstrated that the HSI may be seasonally dynamic (Bateman et al., 2012; Nakazawa et al., 2004; Reside et al., 2010) and that temporal and spatial variations in biotic interactions can affect the results of niche modeling (Wisiz et al., 2013). Our study establishes a link between these two categories of results by demonstrating that the relationship between the HSI and demography is itself strongly variable temporally at an intra-annual scale. One corollary of this is that a static HSI is not sufficient to explain demography.

Our HSI was derived from occurrence data independent from our reproduction data (Monnet et al., 2015). It reflects the propensity of individuals to select various habitat types during the core breeding season. Overall, the Houbara's daily nest survival rate exhibits a strong decrease with the progression of the breeding season (Table 1 and online Appendix B4 in Appendix S2), which is expected with respect to both demographic heterogeneity (e.g., more experienced females tend to lay early in the season and have potentially high breeding success) (Verhulst & Nilsson, 2008), and to meteorological changes along the season, which can also impact nest survival (Verhulst & Nilsson, 2008). Most importantly, nest survival is negatively related to the HSI early in the season, and this relationship becomes weaker with the progression of the season to the extent that it is eventually reversed by the end of the season (Figure 2). Even if this trend presents wide confidence intervals late in the breeding season due to a smaller sample size, the significance of the interaction between *HSI* and *Date* stands as a strong support of the dynamic of the relationship.

It has been suggested that the negative relationships between HSI and demography are related to density-dependent processes which limit demographic performances at high density (Guisan & Thuiller, 2005; Thuiller et al., 2014). Because of the large spatial scale (75,000 km²) and fine temporal scale (intra-seasonal changes in relation to daily nest survival) of our study, we could not obtain accurate estimates of Houbara densities along the breeding season and thus could not formally assess the role of density in the demography–HSI relationship. However, studies on habitat suitability generally have reported significant positive correlation between HSI and population densities (Oliver et al., 2012; Törres et al., 2012). This is in concordance with the positive correlation observed between autumnal densities of Houbaras and the HSI (ECWP unpublished data, see Appendix B5 in Appendix S2). During the breeding season, Houbaras are nonevenly distributed. In this lekking species, males aggregate to display and female nests are spatially associated to lek occurrence (Hingrat et al. 2004; Hingrat, Saint Jalme, Chalah, Orhant, &

Lacroix, 2008) in habitats of highest quality (i.e., with highest HSI). It is therefore likely that the HSI is positively correlated with Houbara densities during the breeding season and that our results reflect a dynamic balance of the positive effect of highly suitable habitat on nest survival, and the negative effect associated with high Houbara density. Similar observations and interpretations have been obtained for survival probabilities of adult Houbaras with an independent data set (Monnet et al., 2015). Importantly, such relationship between demography and HSI mediated by density-dependent processes implies that two types of processes occur: (1) Density is higher in highly suitable habitats (high HSI) (Oliver et al., 2012; Törres et al., 2012), and (2) demographic performance is negatively related with density (Brook & Bradshaw, 2006). Both types of relationships are likely to be temporally variable, in turn leading to temporal variation in the HSI-demography relationship.

In Houbara, the first type of process (i.e., dynamic density-HSI relationship) is likely explained by the cyclical switch of the realized niche of Houbara, in which females use different areas in the breeding and wintering seasons (Hingrat, Saint Jalme et al. 2007). At the transition between the breeding and nonbreeding seasons, the expected correlation between the breeding range HSI and actual occurrence (and density) may disappear or be attenuated, in turn reducing any density-mediated adverse effects on the daily nest survival.

The second type of process (i.e., dynamic relationship between density and demographic rates) is likely related to the dynamics of biotic interactions. During the breeding season, females nesting mostly at the periphery of leks might undergo high levels of male harassment, in turn affecting negatively the time they allocate in feeding trips and in attending the nest (Stone, 1995) or even increasing their detectability to predators (Magurran & Nowak, 1991). Additionally, the high breeding activity and higher Houbara density in high HSI sites can attract more predators (see, e.g., Keyser, Hill, & Soehren, 1998; Larivière & Messier, 1998), inducing higher rates of nest predation (Gunnarsson & Elmberg, 2008; Vickery, Hunter, & Wells, 1992). Observed changes in the nest survival-HSI relationship are consistent with the expected reduction in these antagonist effects along the season. The male displaying season ends sooner than the nesting season (Hingrat, Saint Jalme et al. 2007), meaning females will face lower levels of male harassment toward the end of the season. The decreasing number of nesting females will also reduce competition for nest sites and food resources. Furthermore, Red Fox (*Vulpes vulpes*), the main predators of Houbara nests (Bacon & Hingrat, unpublished data), are expected to change their foraging behavior along the season (Cavallini & Lovari, 1991) in relation to the dynamic abundance of alternative resources such as arthropods (Hingrat, Ysnel et al. 2007) or even bird chicks (rather than eggs).

With the exception of Pellissier et al. (2013), who found a significant relationship between nest success and HSI in the Ruddy Turnstone (*Arenaria interpres*) across years in relation to snow cover, we are not aware of other characterizations of the dynamics of the link between HSI and a demographic parameter. Our results regarding the Houbara indicate that this link can be variable within year, probably

in relation to the dynamics of intra- and interspecific interactions and/or habitat selection, but with a similar pattern between years. Niche modeling has become an increasingly widely used technique in ecology, having been successfully used to address a large range of fundamental and applied research questions (Monnet, Hingrat, & Jiguet, 2015; Yannic et al., 2014). Here, we used a HSI computed over a period covering the core breeding season of Houbaras using powerful analytical techniques (Thuiller et al., 2009). However, in spite of its sophistication, our static HSI does not appear to reflect the complexity of demographic patterns and their intraseasonal dynamics, and using it as a mere proxy for demography would lead to incorrect inferences. Other analytical tools than niche modeling exist to study species distribution, such as the resource selection function (Manly, McDonald, Thomas, McDonald, & Erickson, 2002). Although these tools have been used to study demography (McLoughlin, Boyce, Coulson, & Clutton-Brock, 2006; McLoughlin et al., 2007), it appears that the same limitations occur as for niche modeling (Boyce, Vernier, Nielsen, & Schmiegelow, 2002; McLoughlin, Morris, Fortin, Vander Wal, & Contasti, 2010). In this context, advances in the development of dynamic habitat suitability metrics (Yannic et al., 2014) and the inclusion of dynamic biotic interactions in niche modeling (Wisz et al., 2013) offer promising new approaches to understand the link between HSI and demography. Three important implications of these approaches are the appreciation of the ecological processes that shape species' ranges (Bateman et al., 2012; Thuiller et al., 2008), the understanding of the evolutionary processes driving habitat selection (Battin, 2004; Jones, 2001), and the development of mechanistic models of species distribution (i.e., models describing all important processes potentially constraining a species' range) to provide more accurate predictions than the widely used correlative models (niche modeling) (Buckley et al., 2010; Kearney, 2006; Kearney & Porter, 2009).

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CONFLICT OF INTEREST

None declared.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Supplementary Materials – Article 3

Online Appendix S1: Methods

Online Appendix A1: Number of nests monitored per year

Table A1.1. Nest visit intervals distribution statistics in function of the year and the nest location technique (Transmitter = nest located from females fitted with VHF or satellite transmitters, Shepherd = nests located from a collaboration with local shepherd).

Year	Visit intervals		Mean	Median	Standard deviation	Standard error	1st centile	9th centile	N nests	N visit intervals
	Nest technique	location								
2003	Transmitter		7.45	7.00	4.67	0.65	2.00	14.00	24	51
2003	Shepherd		7.39	7.00	4.73	0.58	1.00	12.00	35	67
2004	Transmitter		9.36	8.00	5.28	0.47	4.00	15.00	68	124
2004	Shepherd		8.60	7.00	5.85	0.39	1.00	17.00	108	220
2005	Transmitter		5.20	5.00	2.37	0.43	2.00	8.10	12	30
2005	Shepherd		5.72	5.00	3.90	0.72	1.80	11.20	14	29
2006	Transmitter		6.74	7.00	3.03	0.25	2.00	10.00	61	149
2006	Shepherd		5.13	4.00	4.25	0.16	1.00	10.00	236	728
2007	Transmitter		5.07	5.00	2.54	0.19	2.00	8.00	59	182
2007	Shepherd		5.74	5.00	4.65	0.34	1.00	13.00	82	192
2008	Transmitter		5.24	5.00	2.81	0.18	2.00	8.00	75	238
2008	Shepherd		5.29	5.00	4.16	0.41	1.00	10.00	43	101
2009	Transmitter		5.02	5.00	2.26	0.21	2.00	7.00	37	115
2009	Shepherd		5.42	5.00	4.28	0.26	1.00	12.00	100	262
2010	Transmitter		5.50	5.00	2.29	0.23	2.00	8.00	38	103
2010	Shepherd		5.06	5.00	3.35	0.19	1.00	9.00	118	325
2011	Transmitter		5.71	6.00	2.35	0.48	1.60	8.00	11	24
2011	Shepherd		5.44	5.00	3.77	0.14	1.00	9.50	287	716
2012	Transmitter		6.05	6.00	2.47	0.31	3.00	8.00	23	62
2012	Shepherd		5.19	5.00	3.30	0.08	1.00	9.00	605	1713
2013	Transmitter		6.24	7.00	3.16	0.47	2.00	9.00	21	46
2013	Shepherd		6.26	6.00	4.34	0.11	1.00	12.00	574	1494
2014	Transmitter		5.16	6.00	2.21	0.44	2.00	7.00	7	25
2014	Shepherd		5.38	5.00	3.55	0.10	1.00	9.80	470	1333

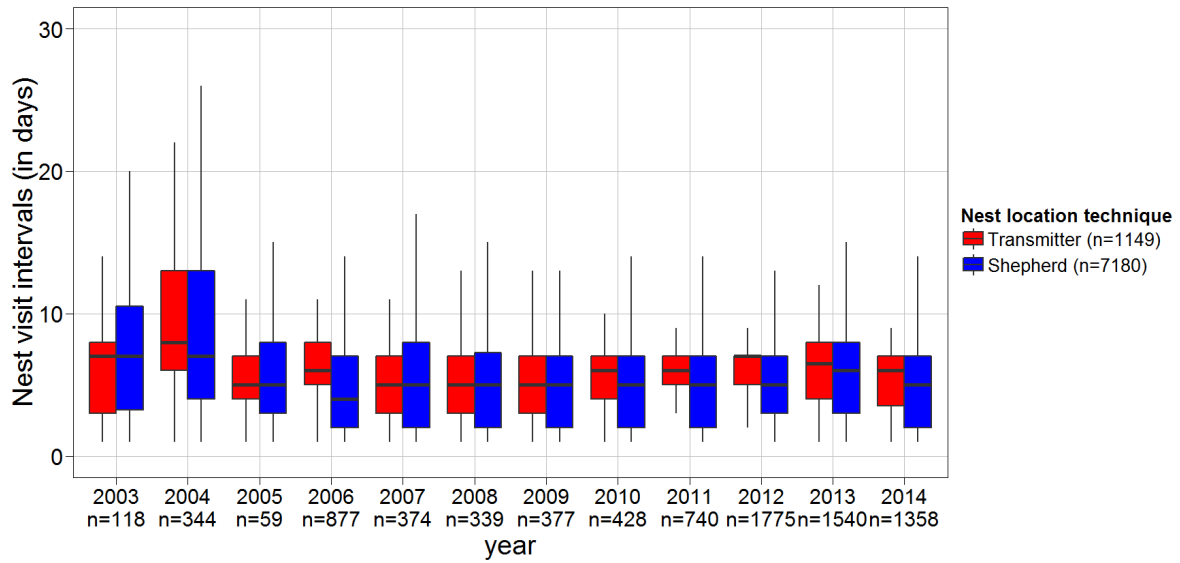


Figure A1.1. Nest visit intervals distribution (boxplot) in function of the year and the nest location technique (Transmitter = in red, nest located from females fitted with VHF or satellite transmitters, Shepherd = in blue, nests located from a collaboration with local shepherd).

Table A1.2. Nest visit intervals distribution statistics in function of the year and the nest monitoring technique (Presence or not of camera trap).

Year	Visit intervals							N nests	N visit intervals
	Presence camera trap	Mean	Median	Standard deviation	Standard error	1st centile	9th centile		
2003	No	7.42	7.00	4.68	0.43	2.00	13.00	59	118
2004	No	8.88	8.00	5.66	0.31	2.00	15.00	176	344
2005	No	5.46	5.00	3.20	0.42	2.00	10.00	26	59
2006	No	5.40	5.00	4.11	0.14	1.00	10.00	297	877
2007	No	5.41	5.00	3.78	0.20	1.00	10.00	141	374
2008	No	5.25	5.00	3.27	0.18	2.00	9.00	118	339
2009	No	5.29	5.00	3.78	0.19	1.00	9.00	137	377
2010	No	5.17	5.00	3.13	0.15	1.00	9.00	156	428
2011	No	5.45	5.00	3.73	0.14	1.00	9.00	298	740
2012	No	5.22	5.00	3.27	0.08	1.00	9.00	628	1775
2013	No	6.24	6.00	4.43	0.12	1.00	13.00	595	1408
2013	Yes	6.41	6.00	2.65	0.23	3.00	10.00	116	132
2014	No	5.16	5.00	3.68	0.11	1.00	10.00	477	1172
2014	Yes	6.70	7.00	1.90	0.14	4.00	8.00	115	186

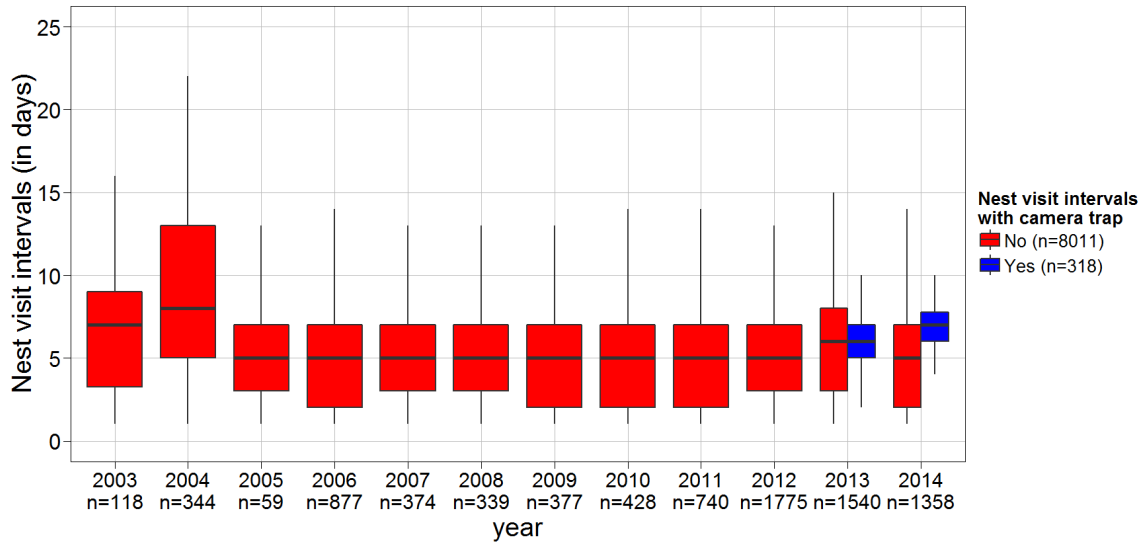


Figure A1.2. Nest visit intervals distribution (boxplot) in function of the year and the nest monitoring technique (Presence (in blue) or not (in red) of camera trap).

Online Appendix A2: Environmental data for species distribution modelling (Monnet *et al.* 2015)

Monnet *et al.* (2015) used both climate and land cover variables for species distribution modelling: the three first axes of a principal components analysis calibrated on eight bioclimatic variables (Table A2.1) and seven land cover variables (Table A2.2).

Table A2.1. Bioclimatic variables from the Worldclim database (Hijmas *et al.* 2005).

Code	Variables
BIO1	mean annual temperature
BIO6	minimum temperature of the coldest month
BIO5	maximum temperature of the warmest month
BIO4	temperature seasonality (standard deviations of mean monthly temperatures)
BIO12	annual precipitation
BIO14	precipitation of the driest month
BIO13	precipitation of the wettest month
BIO15	precipitation seasonality (coefficient of variation of monthly precipitations)

Table A2.2. Summarized land cover variables from global land-cover classes (Mayaux *et al.* 2004).

Global land-cover classes	Summarized land cover variables
Open deciduous shrub land	open shrubland
Sparse grassland	sparse grassland
Croplands (>50%)	cropland
Irrigated croplands	cropland
Tree crops	cropland
Bare rock	bare rock
Stony desert	stony desert
Sandy desert and dunes	sandy desert
Closed evergreen lowland forest	unfavorable
Degraded evergreen lowland forest	unfavorable
Montane evergreen forest (> 1500 m)	unfavorable
Sub-montane forest (>900 m)	unfavorable
Mangrove	unfavorable
Mosaic forest / croplands	unfavorable
Closed deciduous forest (Miombo)	unfavorable
Deciduous woodland	unfavorable
Salt hardpans	unfavorable
Waterbodies	unfavorable
Cities	unfavorable

Online References for Appendix S1

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Online Appendix S2: Results

Online Appendix B1: Habitat suitability index (HSI) distribution at nests locations

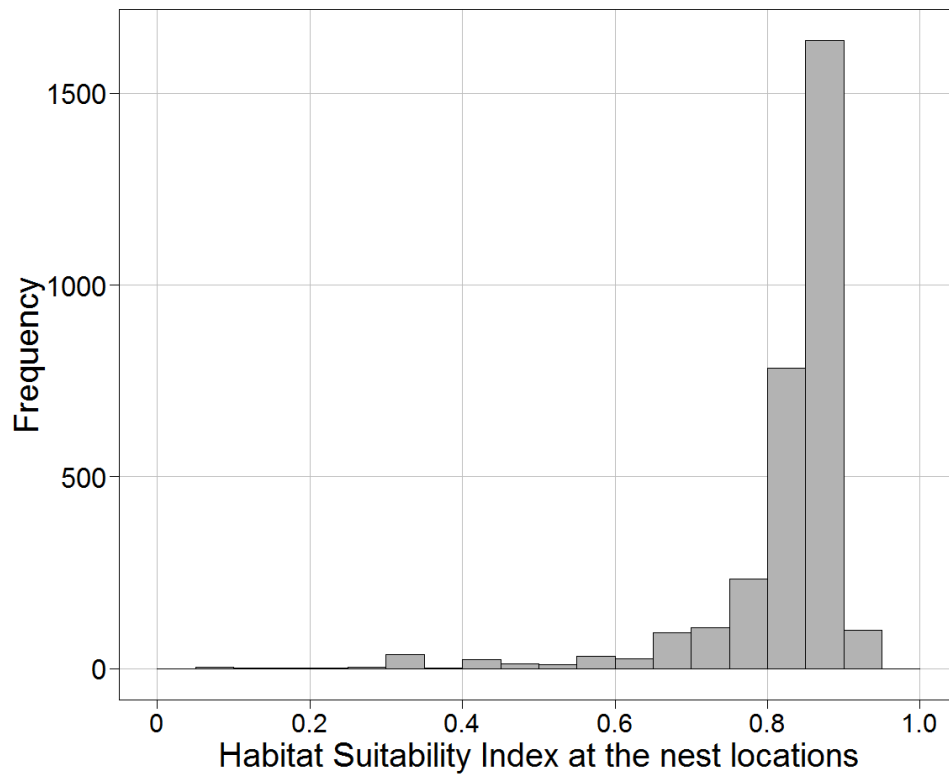


Figure B1. Frequency of the Habitat Suitability Index (HSI) at the nests locations

Online Appendix B2 : Multi-model inference – Model selection

Table B2.1. Model selection from candidates model including combinations of additive effects (Step1). Date = Date within the breeding season, Prec = Average precipitation from the year preceding the breeding season, Temp = Averaged temperature from the year preceding the breeding season, HSI = Habitat suitability index at the nest location. Blank spaces indicate covariates not included in the model. df = degree of freedom, logLik = log likelihood.

Date	Prec	Temp	HSI	df	logLik	AICc	Δ AICc	AICc weight
-0.38	0.09		-0.11	6	-3457.78	6927.60	0.00	0.25
-0.38			-0.11	5	-3458.82	6927.70	0.08	0.24
-0.38	0.09			5	-3459.54	6929.10	1.52	0.12
-0.38	0.10	-0.03	-0.11	7	-3457.63	6929.30	1.69	0.11
-0.38				4	-3460.63	6929.30	1.70	0.11
-0.38		-0.01	-0.11	6	-3458.81	6929.60	2.07	0.09
-0.38	0.09	-0.02		6	-3459.48	6931.00	3.41	0.05
-0.38		0.00		5	-3460.63	6931.30	3.70	0.04
			-0.11	4	-3481.04	6970.10	42.52	0.00
				3	-3482.96	6971.90	44.34	0.00
		-0.01	-0.11	5	-3481.01	6972.00	44.45	0.00
	0.01		-0.11	5	-3481.03	6972.10	44.50	0.00
	0.00			4	-3482.95	6973.90	46.34	0.00
		0.00		4	-3482.95	6973.90	46.34	0.00
	0.01	-0.01	-0.12	6	-3481.00	6974.00	46.43	0.00
	0.00	0.00		5	-3482.95	6975.90	48.34	0.00

Chapitre 3. *Qualité d'habitat et démographie : une relation temporelle*

Table B2.2. Model selection from candidates model including combinations of additive effects and interaction terms (step 2). Date = Date within the breeding season, Prec = Average precipitation from the year preceding the breeding season, Temp = Averaged temperature from the year preceding the breeding season, HSI = Habitat suitability index at the nest location. Blank spaces indicate covariates and interactions not included in the model. df = degree of freedom, logLik = log likelihood.

Date	Prec	Temp	HSI	Date HSI	x	Prec HSI	x	Temp HSI	x	df	logLik	AICc	ΔAICc	AICc wieght
-0.34	0.11		-0.18	0.34						7	-3453.77	6921.50	0.00	0.28
-0.35			-0.18	0.33						6	-3455.04	6922.10	0.55	0.21
-0.35	0.11	-0.03	-0.18	0.34						8	-3453.61	6923.20	1.70	0.12
-0.34	0.10		-0.17	0.36		-0.05				8	-3453.70	6923.40	1.86	0.11
-0.35		0.00	-0.18	0.33						7	-3455.04	6924.10	2.56	0.08
-0.35	0.11	-0.02	-0.19	0.35				0.06		9	-3453.54	6925.10	3.56	0.05
-0.35	0.10	-0.03	-0.18	0.36		-0.04				9	-3453.55	6925.10	3.59	0.05
-0.34		0.00	-0.18	0.33				0.07		8	-3454.94	6925.90	4.35	0.03
-0.34	0.10	-0.02	-0.18	0.36		-0.03		0.05		10	-3453.51	6927.00	5.49	0.02
-0.38	0.09		-0.11							6	-3457.78	6927.60	6.03	0.01
-0.38			-0.11							5	-3458.82	6927.70	6.11	0.01
-0.38	0.11		-0.12			0.09				7	-3457.48	6929.00	7.42	0.01
-0.38	0.09									5	-3459.54	6929.10	7.55	0.01
-0.38	0.10	-0.03	-0.11							7	-3457.63	6929.30	7.72	0.01
-0.38										4	-3460.63	6929.30	7.72	0.01
-0.38		-0.01	-0.11							6	-3458.81	6929.60	8.09	0.01
-0.38	0.11	-0.03	-0.12			0.09				8	-3457.29	6930.60	9.05	0.00
-0.38	0.09	-0.02								6	-3459.48	6931.00	9.43	0.00
-0.38	0.10	-0.03	-0.11					0.03		8	-3457.61	6931.20	9.69	0.00
-0.38		0.00								5	-3460.63	6931.30	9.72	0.00
-0.38		-0.01	-0.11					0.04		7	-3458.78	6931.60	10.03	0.00
-0.38	0.11	-0.03	-0.13			0.11		0.07		9	-3457.20	6932.40	10.89	0.00
			-0.11							4	-3481.04	6970.10	48.55	0.00
										3	-3482.96	6971.90	50.37	0.00
		-0.01	-0.11							5	-3481.01	6972.00	50.48	0.00
	0.01		-0.11							5	-3481.03	6972.10	50.52	0.00
	0.03		-0.13			0.11				6	-3480.54	6973.10	51.54	0.00
		-0.01	-0.12					0.08		6	-3480.85	6973.70	52.17	0.00
	0.00									4	-3482.95	6973.90	52.37	0.00

	0.00				4	-3482.95	6973.90	52.37	0.00
0.01	-0.01	-0.12			6	-3481.00	6974.00	52.46	0.00
0.03	-0.02	-0.13	0.12		7	-3480.48	6975.00	53.43	0.00
0.01	-0.01	-0.12		0.08	7	-3480.84	6975.70	54.16	0.00
0.00	0.00				5	-3482.95	6975.90	54.37	0.00
0.03	-0.01	-0.14	0.15	0.14	8	-3480.08	6976.20	54.62	0.00

Online Appendix B3: Consistency of HSI × Date among years

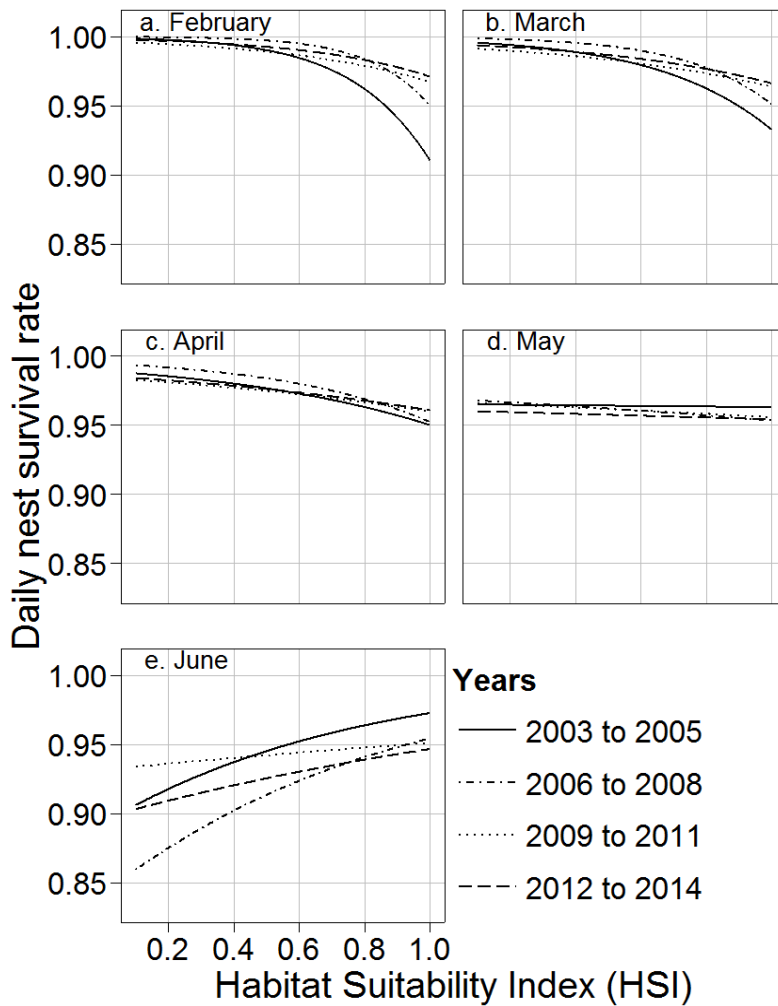


Figure B3. Relationship between the daily nest survival rate and the Habitat Suitability Index (HSI), with inter-annual grouping for each month of the breeding season. a. February, b. March, c. April, d. May and e. June.

Online Appendix B4: Daily nest survival rate (\pm 95% CI) along the breeding season for various values of Habitat Suitability Index (HSI).

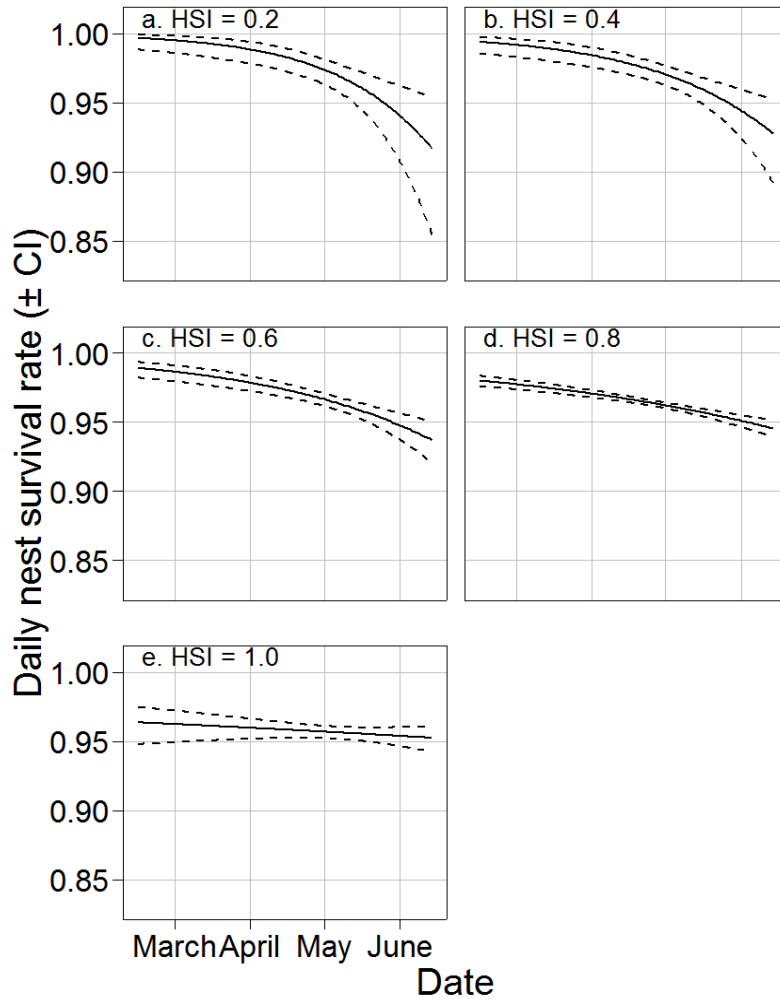


Figure B4. Relationship between the daily nest survival rate (\pm 95% CI) and the date within the breeding season for different values of Habitat Suitability Index (HSI). a. HSI = 0.2, b. HSI=0.4, c. HSI=0.6, d HSI=0.8, and e. HSI=1.0.

Online Appendix B5: North-African Houbara Bustard (*Chlamydotis undulata undulata*)

autumn densities in function of intervals of Habitat Suitability Index (HSI).

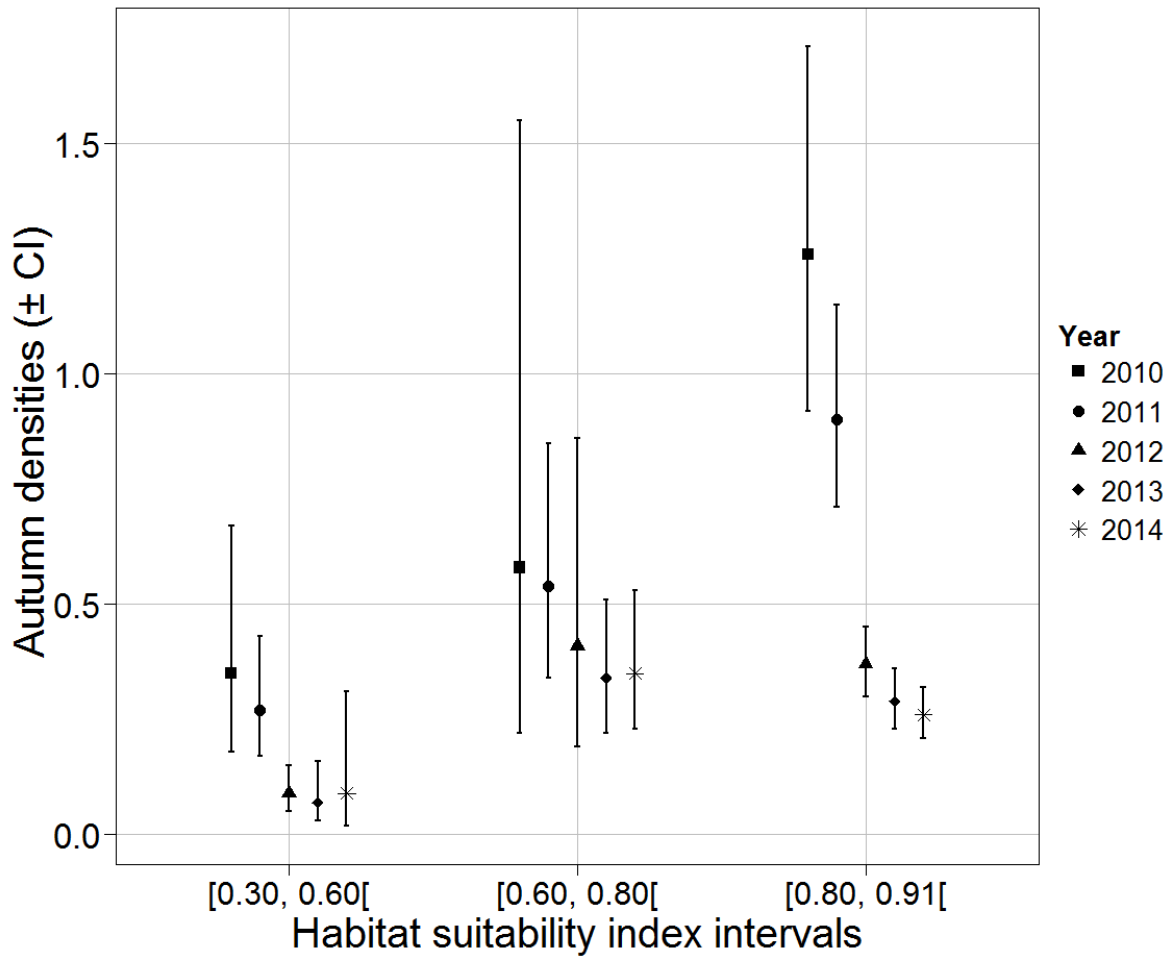


Figure B5. North-African Houbara bustard (*Chlamydotis undulata undulata*) autumn densities (\pm 95% confidence intervals) in function of Habitat Suitability Index intervals.

Chapitre 4. Renforcement, protection et gestion cynégétique de l'outarde Houbara nord-africaine : une évaluation de la dynamique de la population

Résumé

Généralement, le succès au long terme d'un programme de translocation conservatoire peut se caractériser par la capacité des individus issus des translocations à survivre et à produire des descendants viables et productifs permettant la stabilité et la persistance de la population sans actions de translocations additionnelles. Nous avons étudié les conséquences démographiques du renforcement d'une population d'outarde Houbara nord-africaine, qui repose sur d'importants lâchers répétés d'individus produits en captivité dans une aire de conservation mixte (subdivisée en zones de chasse et de réserve). A l'aide d'analyses de viabilité des populations, nous avons tenté de déterminer comment l'effort de renforcement et la pression de chasse actuels affectent la dynamique de la population et sa probabilité d'extinction faisant l'hypothèse d'un arrêt des actions de renforcement. Nos résultats indiquent que (1) sous les conditions actuelles, et sans renforcement, la population décroît de manière déterministe et s'éteint rapidement, même en l'absence de chasse. (2) Néanmoins, le programme de renforcement a un effet positif sur la dynamique de la population, non seulement par les importants effectifs lâchés, mais aussi par la reproduction des individus lâchés et la contribution de leur progéniture sur la croissance démographique. En particulier, les importants effectifs lâchés permettent d'atteindre une taille de population qui réduit les risques d'extinction à court terme, même après l'arrêt des renforcements. Bien que la population d'outarde Houbara ne soit pas viable sur le long terme sans des interventions de renforcement, le programme de renforcement apparaît comme un outil de conservation efficace pour préserver l'espèce jusqu'à ce que les menaces liées à son environnement aient été traitées de manière adéquate.

Mots-clés : Chasse, dynamique de population, translocation conservatoire, Vortex

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**Article 4. Reinforcement, protection and hunting management of the
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Article en préparation pour *The Journal of Wildlife Management*

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Reinforcement, protection and hunting management of the North-African Houbara bustard. A population dynamic assessment.

Léo Bacon^{a, b, *, **}, Alexandre Robert^b, Loïc Hardouin^{a, b}, Yves Hingrat^{a, c}

^aEmirates Center for Wildlife Propagation, PO Box 47, 33250 Missour, Morocco

^bCentre d'Ecologie et des Sciences de la CONservation (CESCO UMR 7204), Museum National d'Histoire Naturelle, CP 135, 43 rue Buffon, 75005 Paris, France

^cRENECO International Wildlife Consultants LLC., Po Box 61741, Abu Dhabi, U.A.E.

*Corresponding author (bacon.leo@gmail.com)

**Orcid ID: 0000-0003-1200-9902

Key-words: conservation translocation, hunting, population dynamics, Vortex

Abstract

The success of conservation translocation programmes is commonly defined as the capacity of translocated populations to persist without further intervention. We investigated the demographic consequences of the North-African Houbara reinforcement programme, which relies on repeated large releases of captive-bred individuals into a mixed conservation area with regular hunting and non-hunting zones. Using population viability analysis, we aimed to assess how the reinforcement effort and hunting pressure affect the current dynamics of the population and its extinction probability assuming cessation of the reinforcement. Our results indicate that (1) under current conditions, without reinforcement, the population would be deterministically decreasing and would rapidly go extinct, even in the absence of regular hunting. Thus, although hunting pressure decreases the time to extinction, other factors are determinant and must be addressed in the conservation strategy to establish a viable Houbara population. (2) Nevertheless, the reinforcement programme has positive effect on population dynamics, not only due to large releases, but also to the reproduction of translocated individuals and the contribution of their offspring to population growth. In particular, large numbers of releases allow reaching population sizes that reduce the risk of short term extinction even after the cessation of releases. Therefore, although the reinforced Houbara population is not viable without intervention in the long run, the reinforcement programme

appears as an efficient conservation tool to preserve the species from extirpation before key environmental factors can be adequately addressed.

Introduction

Translocations are defined as the deliberated and mediated movement of organisms, from any source, captive or wild, from one area to free release in another (Ewen et al. 2012). Animal translocations have various purposes, including commercial objectives, as the introduction of freshwater fish for sport (Cambray 2003) or the reinforcement (also called restocking or supplementation) of wild populations for their exploitation (Champagnon et al. 2012, 2013). Among this variety of approaches, some translocation programmes, often based on large releases, have only recreational purposes (e.g. immediate put and take hunting, Sokos et al. 2008) and do not aim to establish or reinforce a breeding population (Champagnon et al. 2012). On the other side of the translocation spectrum, conservation translocations generally aim at the reestablishment of population that disappeared from their historical range (in the case of reintroductions) or the reinforcement of declining populations (in the case of reinforcements) (Ewen et al. 2012, Seddon et al. 2014).

The success of conservation translocation programmes is commonly defined as the capacity of translocated populations to persist without further intervention (Ewen et al. 2012, IUCN 2013). Ideally the assessment of the long-term viability of translocated populations is based on quantitative population viability assessments (Robert et al. 2015a). However, such assessment is rarely achieved mainly due to the lack of appropriate monitoring and difficulties in data analysis (Fischer & Lindenmayer 2000, Sutherland et al. 2010). Translocated populations are complex, heterogeneous and unbalanced systems characterized by a mix of released and wild-born animals with potentially distinct and heterogeneous demographic rates. In such systems, short and middle term dynamics and viability are non-trivial and their assessment requires integrating all sources of heterogeneity of the reinforced population (spatial and temporal heterogeneity as well as potential differences among individual of various sexes, ages and origins).

The North-African Houbara bustard (*Chlamydotis undulata undulata*, hereafter Houbara) is a medium size bird distributed from North Mauritania to Egypt, threatened by over-hunting, poaching and habitat degradation, which have led to the decline of the species during the second half of the twentieth century (Goriup 1997). This decline led to the creation, in 1995, of the Emirates Center for Wildlife Propagation (ECWP) based in Eastern Morocco (Lacroix

et al. 2003). Relying on a captive breeding programme and on regular releases of captive-bred individuals, combined with ecological research and hunting management, the ECWP aims to increase the population size of the threatened Houbara throughout its range, to establish viable and sustainable populations in adequacy with the persistence of traditional Arab falconry hunting (Lacroix et al. 2003). The Houbara population management scheme of the ECWP system is based on a mixed conservation area (see discussion in Hardouin et al. 2015) with hunting and non-hunting areas both reinforced with regular releases of captive-bred Houbaras. Released Houbaras have been found to exhibit heterogeneous demographic rates between the hunting and non-hunting areas (survival and dispersal probabilities, Hardouin et al. 2015). Furthermore, based on the longitudinal survey of the population, the variations of survival probabilities and breeding parameters with age, sex and between wild-born and released individuals have been assessed within previous analyses (Bacon et al. 2017, Hardouin et al. 2014, 2015, ECWP unpublished data). Here we conduct a population viability analysis (see Beissinger & McCullough 2002) to assess the effect of the ECWP reinforcement programme on Houbara population dynamics, with three main objectives:

- 1- First, we study the viability of the reinforced population under current management conditions at different temporal scales and assess if the population can persist without further reinforcement actions.
- 2- Second, we assess how reinforcement effort and hunting pressure affect the dynamics and extinction probability of the population.
- 3- Third, like many translocation programmes with hunting purposes (e.g., ring necked pheasants, mallards), the ECWP programme relies on large and repeated releases (several 1000s of individuals per year) to compensate hunting yields. However, unlike most translocations for hunting, the ECWP releases aim at establishing a breeding population (see Bacon et al. 2017). Then, beyond the mere question of the viability of the system, we also assess the contribution of breeding of released individuals on the dynamics of the whole system, by comparing the dynamics of the reinforced population (with empirically assessed breeding parameters) with the dynamics under a model assuming that the released individuals do not breed (hereafter referred to as the “non-breeding model”).

Material and methods

Study species, intervention area and reinforcement programme

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The Houbara is a medium-sized bird inhabiting semi-desert steppes of North Africa. The species is classified as vulnerable within the IUCN red list (Birdlife International/IUCN 2016). It is a non-migratory species presenting an exploded lek mating system (Hingrat et al. 2008). Females are ground-nesting, and lay generally two to three eggs that they incubate for 23 days on average. In case of nest failure, females may initiate a replacement clutch. Houbara chicks are nidifugous and fledge at the mean age of 60 days (Hardouin et al. 2012). The breeding season ranges from mid-February to mid-June. Males generally start reproducing later (2 – 4 years old) than females (1 – 4 years old). Maximum longevity observed in the wild was at least 13 years old for a wild-born breeding female and 15 years old for a wild-born breeding male (ECWP unpublished data).

The severe decline of the Houbara population over the last decades led to the establishment of the Emirates Center for Wildlife Propagation in Morocco in 1995. A comprehensive strategy combining protection, reinforcement using captive-bred Houbara individuals and hunting management was established over an intervention area, in Eastern Morocco, cumulating over 50 000 km². The intervention area is characterized by an arid climate marked by irregular rainfalls (less than 200 mm/year). Mean temperatures varied from 6.80°C in winter (December to February) to 26.64°C in summer (June to August). The habitat in the intervention area is characterized by sparse shrubby vegetation. Two ECWP breeding stations were established for captive breeding (in Missouri in 1995 and in Enjil in 2005, see online appendix A). A detailed description of the captive breeding programme can be found in Lesobre et al. (2010) and Chargé et al. (2010, 2014). Hunting was banned between 2000 and spring 2005 and then restricted to the autumn and winter period (October–January) in 60% of the intervention area, i.e. outside of protected areas. From 1996 to 2016, 108 486 birds were released in North Africa (94 374 in the intervention area). Within the intervention area, the overall number of birds released progressively increased over the years (from 28 in 1996 to 9 084 in 2016, see online appendix B and Hardouin et al. 2014). Houbaras are released at an average of 6 ± 3 (standard deviation) months of age in autumn (August to December), 9 ± 1 months of age in spring (February to May). Autumn releases were managed to avoid direct mortality and disturbance due to hunting. In addition, since 2003, some birds were released in summer (June) at an average of 3 ± 0.6 months of age.

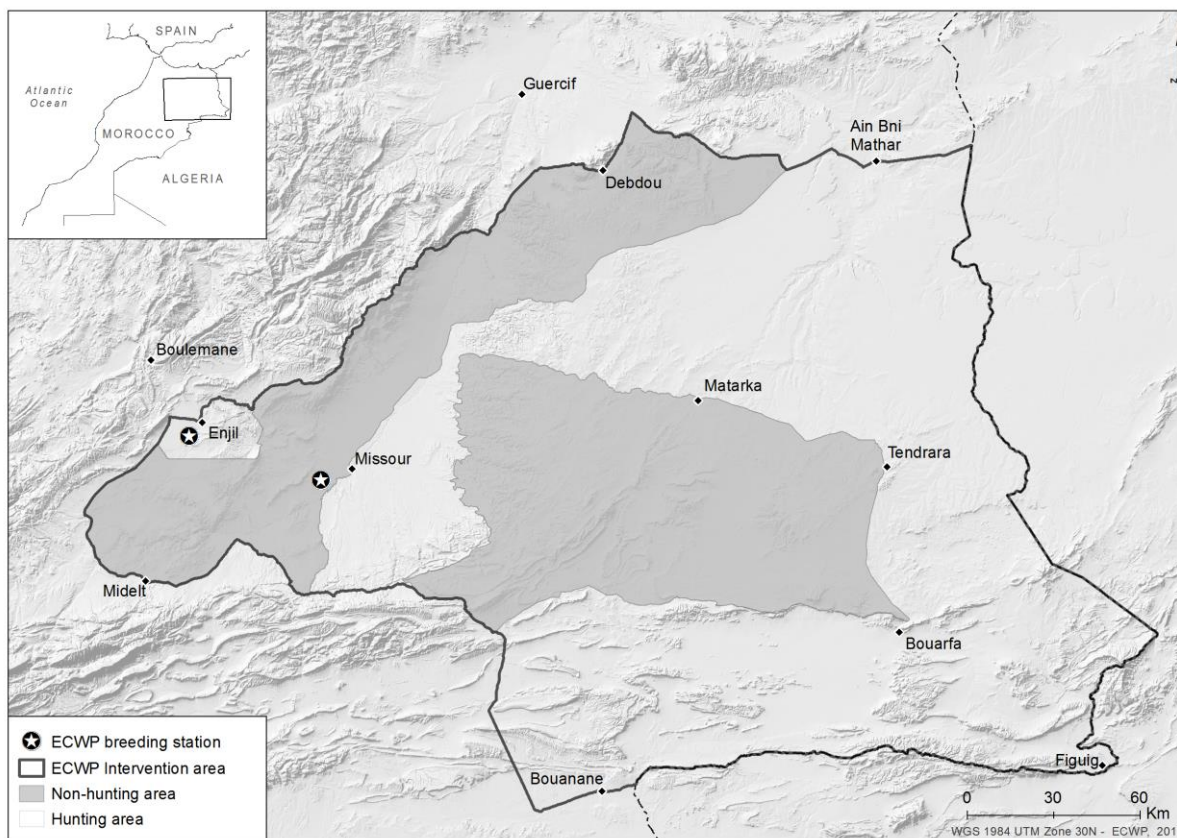


Figure 1. ECWP intervention area partitioned within hunting (30 348 km²) and non-hunting (19 862 km²) areas.

Population models

Deterministic model

We first developed a post-breeding female-based stage structured matrix model (Caswell 2001) with a yearly time step. It was set to explore population dynamics of wild-born individuals in the absence of translocation and hunting. This matrix model considered 14 age classes with reproduction starting at one year of age. Survival rates were estimated from the monitoring of wild-born females fitted with transmitters (ECWP unpublished data, Table 1). Productivity was defined as the number of juveniles produced per female. Juveniles were tallied as the number of chicks that reached the age of fledging (60 days of age). Bacon et al. (in prep.) observed varying breeding performances depending on female origin for brood survival and nesting effort (i.e., the product of the breeding probability and the number of nests initiated for breeding females). Yet, these differences are dependent on translocation strategies and precise age dependent patterns for wild-born females are lacking. Therefore, to keep our analysis simple and conservative, we assigned age dependent productivity rates of captive-bred released females to wild-born cohorts (Table 2). The productivity was calculated

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as the product of estimated breeding parameters obtained from the monitoring of captive-bred released females over the breeding seasons 2002 to 2016 (Table 2, Bacon et al. 2017 and ECWP non-published data). The fertility transition rate was then estimated for each age class as the product of the survival probability of the female to the next age class, its productivity and a sex ratio of 0.5 at birth (see online appendix C). Population growth rate and generation time were estimated from the obtained Leslie matrix using the R package “popbio” (Stubben et al. 2016, R Development Core Team 2017). Popbio package was then used to conduct elasticity analysis, to assess the effect of a proportional change in life history parameters (survival and fertility) on the growth rate of the population. To complement the classical elasticity analysis, we considered additional scenarios in which we replaced our averaged estimates of productivity and survival parameters observed over the study period with minimum and maximum observed annual values (see online appendix D and details in results).

Table 1. Survival probabilities of Houbara bustard as functions of their origin and location (for males and females).

Origin/Location	Age interval			
	0-1 (juvenile)	1-2	2-3	3+
Wild-born	0.44	0.44	0.89	0.89
Hunting area		0.19	0.45	0.65
Captive-bred		0.69	0.79	0.87
Non-hunting area				

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Table 2. Breeding parameters values and productivity of captive-bred females released in the wild as functions of their age.

Breeding parameters	Age of females									
	1	2	3	4	5	6	7	8	9	10-13
Probability of breeding ¹	0.08	0.5	0.63	1	1	1	1	1	1	1
Number of nest initiated (for breeding females)	1.33	1.33	1.33	1.73	1.73	1.73	1.73	1.73	1.73	1.73
Clutch size	2.29	2.4	2.44	2.46	2.47	2.46	2.43	2.38	2.31	2.23
Nest survival probability	0.54	0.54	0.54	0.54	0.54	0.54	0.54	0.54	0.54	0.54
Hatching rate	0.81	0.81	0.81	0.81	0.81	0.81	0.81	0.81	0.81	0.81
Brood survival probability	0.11	0.24	0.37	0.46	0.51	0.54	0.55	0.57	0.57	0.57
Fledging rate	0.65	0.65	0.65	0.65	0.65	0.65	0.65	0.65	0.65	0.65
Productivity ²	0.01	0.11	0.22	0.56	0.62	0.65	0.66	0.67	0.65	0.63

¹Probability of breeding = probability for a female to initiate at least one nest within a breeding season. The product of the probability of breeding and the number of nests initiated is defined as the nesting effort (the number of nests initiated per female per breeding season). ²Productivity = product of all breeding parameters listed in table 2.

Extinction risk of reinforced population

As a second step, we built age and sex structured stochastic population models using Vortex10 (Lacy et al. 2015).

- Reproductive system

We defined our population system with females starting to reproduce at one year of age and males at three. The maximum age for female and male reproduction was respectively 13 and 15 and the maximum lifespan was set to 15 for all individuals. We defined the maximum number of broods per year to 1 and the maximum number of offspring per brood to 8. Although females can have more than one brood per year we considered only one brood per year and adjusted estimates accordingly (Lacy et al. 2015). We defined the maximum number of offspring as the sum of two broods with 4 offspring each (theoretical maximum number of offspring per brood).

- Dispersal, mortality and reproductive rates

Within the intervention area, Hardouin et al. (2015) observed asymmetrical dispersal between hunting and non-hunting areas. Movement probabilities were higher from the non-hunting to

the hunting areas than vice versa, even in years without hunting. Based on Hardouin et al. (2015)'s results and fate diagram calculation, we computed yearly age and sex specific dispersal probabilities between non-hunting and hunting areas (Table 3, see online appendix E for detailed calculations).

Table 3. Proportion of individuals dispersing between hunting and non-hunting areas.

Dispersal		Age	
		1	2+
Hunting to Non-hunting	Male	0.1	0.1
	Female	0.09	0.09
Non-hunting to Hunting	Male	0.21	0.17
	Female	0.37	0.47

Mortality probabilities were obtained from the monitoring of wild-born and released captive-bred fitted with transmitters (ECWP unpublished data). We specified age and origin (wild-born or captive-bred) dependent mortality probabilities. Hardouin et al. (2015) observed lower survival of captive-bred released individuals within hunting areas than in non-hunting areas independent of mortality due to hunting. Therefore, mortality rates of captive-bred released females were dependent on their location (hunting or non-hunting area, Table 1). We considered a moderate value of standard deviation (SD) caused by environmental stochasticity of 0.1 for mortality rates (see discussion in Kendall 1998).

Reproductive rates were estimated from the monitoring of captive-bred released females during the breeding season (Table 2). Reproductive rates were compartmented between the probability of female breeding and the number of offspring per breeding female per brood (product of all other breeding parameters). As for survival probabilities, we assigned a standard deviation of 0.1 due to environmental stochasticity for the percentage of female breeding. For the number of offspring per breeding female per brood, we estimated the standard deviation for each age class assuming a Poisson distribution.

- Population size and carrying capacity

Every autumn, after breeding and before releases, the ECWP conducts large scale Houbara counts (circular observations along point transects, Bibby et al. 2000). Observation data are analysed using DISTANCE 7.0 (Thomas et al. 2010) to estimate the population size within the intervention area. We selected the 2016 autumn Houbara population size estimates in

hunting and non-hunting areas (respectively 11 039 and 4 413 individuals) as the initial population sizes for our simulations (see online appendix F). The proportion of captive-bred released individuals within the population (85%) was estimated from hunting bags individual identification conducted between 2014 and 2016 (see online appendix G).

We selected the highest population estimates between 2001 and 2016 (see details in online appendix F) as the carrying capacities within hunting and non-hunting areas.

- Inbreeding depression and catastrophes

We did not incorporate the effects of inbreeding depression because our computing capacities were insufficient for such modelling when assuming potentially large population sizes (several 10 000s individuals). Assuming such large population sizes, no systematic inbreeding and relatively short projection time scales (i.e., 100 years, less than 20 generations), we considered that no strong population dynamics bias is expected from not considering inbreeding depression.

We incorporated high intensity environmental catastrophes, assuming a 90% reduction of survival and reproduction parameters. Based on generic estimates of Reed et al. (2003), we considered that such events occur stochastically with a per generation frequency of 1%, corresponding to a 0.13% annual probability of occurrence.

- Hunting and reinforcement scenarios

Currently, approximately 10 000 birds are released every year without biased sex-ratio and about 2000 birds are hunted per hunting season. The reinforcement effort is allocated to 54% in hunting areas and 46% in non-hunting areas. In VORTEX, all released birds were implemented as one year old individuals. Because captive-bred Houbaras are, in reality, released before one year of age on average, we considered a cost of release directly reducing the number of released birds. Using short-term post release survival estimates from Hardouin et al. (2014), this cost was accounted as an additional mortality probability of released individuals of 45% in average for autumn releases (which represented 42% of total releases) and of 14% in average for spring releases (58% of releases). The age distribution of hunted birds was based on hunting bags individual identification (see details in appendix G). We assigned an equal sex-ratio for hunted birds (Hardouin et al. 2015).

- Equilibrium population size and extinction probabilities

Assuming constant and perpetual hunting pressure and reinforcement effort, our model allowed us to observe the long term properties of the managed system in which the combined effects of intrinsic population dynamics, regulation, hunting and reinforcement lead to a quasi-equilibrium population size. Such population size was reached in less than 25 years in all cases.

Additionally, we ran simulations to compute extinction probabilities after the cessation of the reinforcement programme. Models integrating releases and hunting were run for 25 years (to reach quasi equilibrium), then after the 25 year burn-in we removed reinforcement (Scenario 1) or reinforcement plus hunting pressure (Scenario 2) and computed extinction probabilities along the following 100 years.

Several management scenarios were explored based on scenario 2, with variation in hunting pressure (number of birds hunted per year) and release intensity (number of birds released per year) before cessation. All these scenarios considered empirically observed demographic rates (survival, reproduction and dispersal between hunting and non-hunting areas) for both released and wild-born individuals. Alternatively, we considered *non-breeding scenarios* in which captive-bred individuals did not breed in the wild to assess the contribution of the reproduction of released individuals to the global dynamics of the system and to the mitigation of extinction risk.

In all scenarios, equilibrium population sizes and extinction probabilities were computed based on 100 independent iterations. Extinction probabilities were computed (after a 25 years burn-in followed by the cessation of reinforcement) after 10, 20, 50 and 100 years and local (population) conservation status based on the IUCN red list categorization (criteria E, IUCN 2012) were determined.

Results

Deterministic model: population of wild-born individuals

The analysis of the deterministic model indicated that, in the absence of releases and hunting, the wild-born population is strongly decreasing at demographic equilibrium ($\lambda=0.869$). The generation time is equal to 7.83 years. The elasticity analysis indicated that population growth is strongly sensitive to variation of survival (sum of elasticities for survival ≈ 0.88 , see online appendix H) as compared with fertility parameters (sum of elasticities for fertility parameters

≈ 0.11). Juvenile and one year old individual survival represented almost one quarter of growth rate elasticities (appendix H).

Replacing the average demographic parameters of adults of two years and older (2+ individuals) by extreme annual parameters observed over the study period always resulted in deterministically decreasing populations (λ ranged between 0.60 and 0.93 when replacing survival probabilities of 2+ individuals by extreme survival values and between 0.78 and 0.91 when replacing productivity values for fertility calculation by extreme values). In contrast, increasing the survival probabilities of juvenile and 1 year old individuals by the values observed in 2+ individuals, resulted in a deterministically increasing population ($\lambda=1.04$).

Extinction risks

From the “actual scenario” (i.e., assuming constant and perpetual hunting pressure and reinforcement effort, equal to current values), the average estimated size of the reinforced Houbara population was 12 830 (total SD = 478) (fig 2).

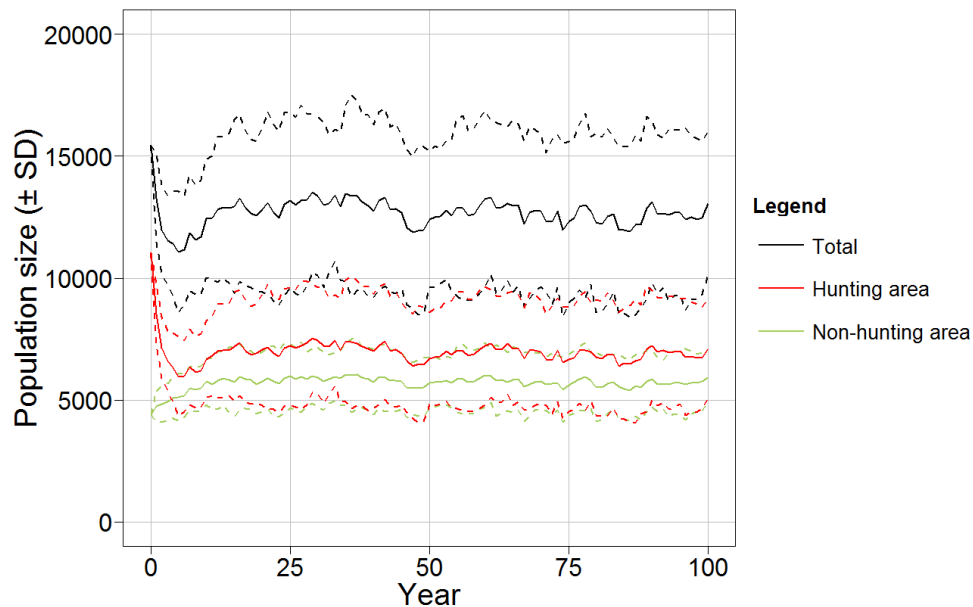


Figure 2. Projected Houbara population size (total and compartmented between hunting and non-hunting areas) with the current reinforcement effort and hunting pressure over a 100 year time span.

The cessation of the reinforcement (implemented at $t=25$ years on Fig. 3) resulted in a strong decrease and rapid extinction of the population (median time to extinction, MTE, following the end of the reinforcement was 17 years with continuing hunting and 58 years when assuming that hunting stopped at the cessation of the reinforcement). Extinction risks

following the end of reinforcement at 10, 20, 50 and 100 years were 0%, 90%, 100% and 100% with continuing hunting and 0%, 0%, 24% and 100% when hunting stopped with reinforcement.

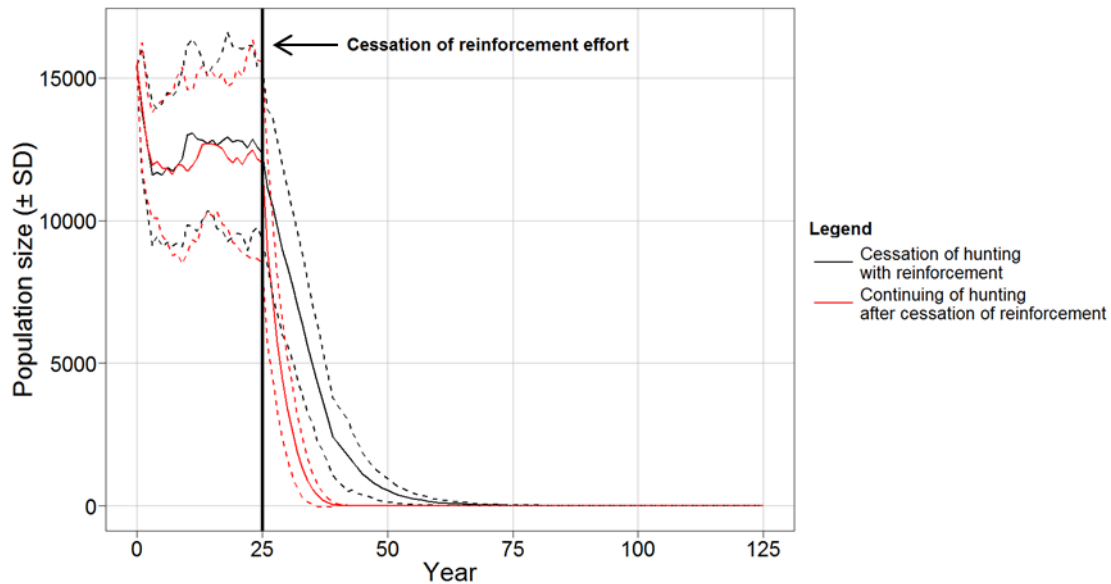


Figure 3. Projected population size with cessation of reinforcement effort after 25 years

Importantly, however, the dynamics of extinction risks after the cessation of the reinforcement was mostly dependent on the release intensity before reinforcement cessation (Fig. 4 left) and only marginally dependent on the hunting pressure during the course of the reinforcement programme (Fig. 5 left).

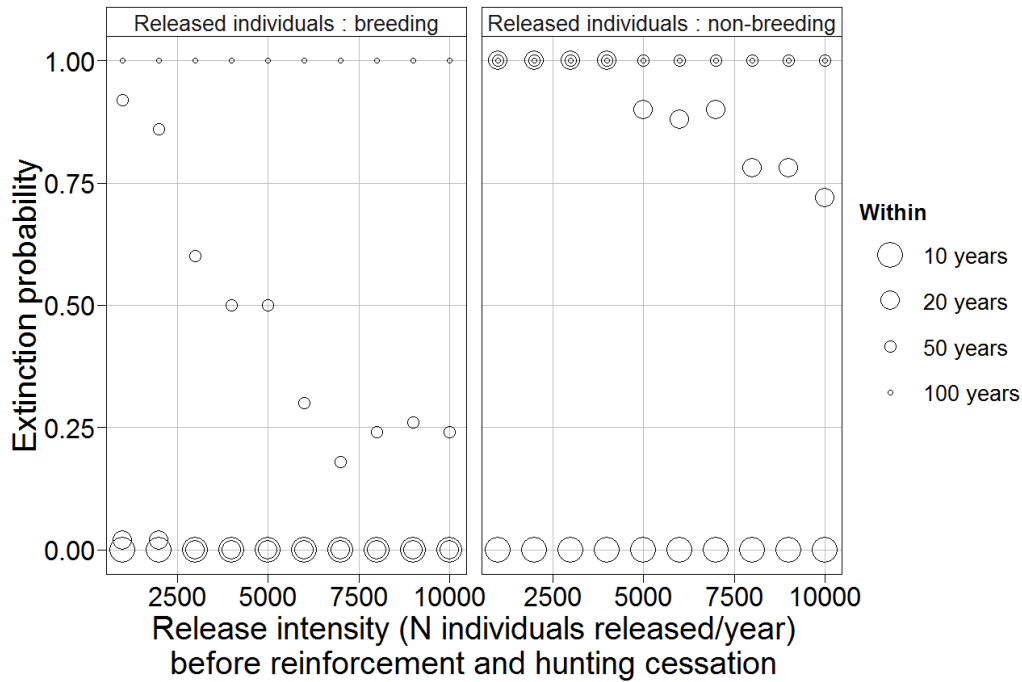


Figure 4. Extinction probabilities after 10, 20, 50 and 100 years for varying release efforts and constant hunting pressure (2000 individuals per year) before reinforcement and hunting cessation. The models assume that released individuals can breed (left) or not (non-breeding scenario, right).

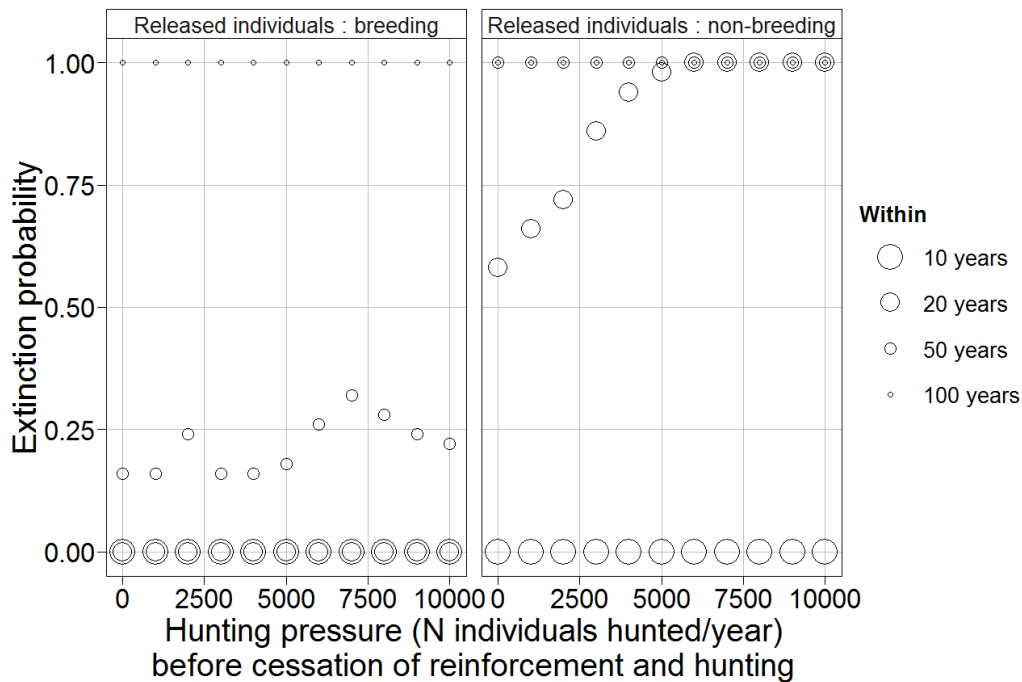


Figure 5. Extinction probabilities after 10, 20, 50 and 100 years for constant release effort (10 000 individuals per year) and varying hunting pressure before reinforcement and hunting cessation. The models assume that released individuals can breed (left) or not (non-breeding scenario, right).

In the non-breeding scenario (Fig. 4 right and 5 right), the cessation of reinforcement and hunting resulted in a strong decrease and rapid extinction of the population (MTE with actual reinforcement and hunting pressure for the first 25 years was 14 years, extinction risks at 10, 20, 50 and 100 years were respectively 0%, 72%, 100% and 100%).

Discussion

The development of population models of the reinforced Houbara population have highlighted two aspects its dynamic. First, it appears that without reinforcement, the population is deterministically declining even in the absence of hunting pressure, underlining the role of potential environmental issues. Second, even if the population do not persist on the long term without releases, current reinforcement actions have a positive effect on population persistence.

Environmental issues

In the absence of any management (no hunting, no reinforcement), the Houbara population would be severely declining and would rapidly go extinct (MTE=58 years under the actual scenario). Individual life history parameters of the Houbara population appear similar as or even higher than some populations from other threatened bustard species, as the great bustard (*Otis tarda*, Lane & Alonso 2001) or the little bustard (*Tetrax tetrax*, Inchausti & Bretagnolle 2005). Without immigration or human intervention, it appears those populations are also declining and at risk of extinction, at the local scale, within a few decades.

The elasticity analysis suggests that management efforts should be directed to improving the survival of individuals within their first two years of life in the wild, which has been shown to be very sensitive to environmental stochasticity in released Houbaras (Hardouin et al. 2014) and potentially to density dependent processes (Azar et al. 2016, Hardouin et al. 2015). As our survival estimates are independent from mortality caused by hunting, it appears that multiple factors come at play in the decline of the population.

As stated for little and great bustards (Bretagnolle & Inchausti 2005, Lane & Alonso 2001), habitat degradation is considered a threat to Houbaras (Chammem et al. 2003, Le Cuziat 2005). Semi-desertic and desertic habitats are prone to large scale and rapid degradation and desertification caused by anthropogenic activities and climate change (Frenette-Dussault et al. 2013, Le Houérou 1995). Monnet (2014) predicted, within the next 50 years, a northward shifting of suitable habitats for Houbara with a severe shrinkage in the South where

populations currently occur, caused by climate and land cover changes. This shift may have been an ongoing process for decades already, regarding empirical knowledge of habitat degradation and desertification within North Africa (Le Houérou 1995, 1996, 2002). The northward shift of Houbara distribution is restrained by geographical barriers (Mediterranean Sea and Atlas Mountain) and human footprint, which may constrain Houbara distribution within habitats that are less suitable than few decades ago. The question today is: are these habitats suitable enough to sustain viable populations? More locally, intensive releases over the last two decades could have negatively impacted individual life history parameters. Strong densities of Houbaras may generate unfavourable conditions, with increasing intraspecific competition (Azar et al. 2016). In United Arab Emirates, long-term survival of released Macqueen bustard (*Chlamydotis macqueenii*) is negatively influenced by subsequent releases events, potentially caused by density dependent mechanisms (Azar et al. 2016).

We did not consider the possibility of dispersal outside the intervention area, which might influence population dynamics. However, (1) even if Houbaras can travel long distance (Hingrat et al. 2005), emigration outside the intervention area has rarely been observed (Monnet et al. 2015, ECWP unpublished data), (2) conservation actions in surrounding areas and countries are significantly less developed or inexistent and Houbara densities are expected to be low (Chammem et al. 2003).

Hunting & reinforcement

Our results clearly emphasize that in the absence of reinforcement, hunting represents a major threat to the persistence of the population (Keane et al. 2005, see Fig. 3). Without reinforcement actions, the population would be considered “endangered” under IUCN classification criteria E (probability of extinction $\geq 20\%$ in 20 years, IUCN 2012). However, combinations of hunting and reinforcement allow reaching large population sizes under a wide range of realistic conditions, including the actual situation encountered in the ECWP mixed conservation area (Fig. 2). Our analysis indicates that not only does the reinforcement programme prevent the population from extinction as long as the programme lasts, but it also allows reducing the risk of rapid extinction after programme cessation owing to the large equilibrium population sizes. Importantly, successful reproduction of captive-bred released Houbaras in the wild (Bacon et al. 2017) contribute to reduce the time to extinction. When considering that released individuals do not breed (non-breeding scenario), the population exhibits much more severe decline and higher extinction risk than under the breeding,

empirical scenario. Under the non-breeding scenario, variation in the release intensity only marginally influences the extinction rate and only at very short time horizon, which let us think that a reinforcement strategy of large releases with the only purpose of absorbing hunting pressure (Sokos et al. 2008) is not relevant in the context of our population.

Management implications

The ECWP is one of the major programmes of the International Fund for Houbara Conservation (www.houbarafund.org) which aims to restore a self-sustainable population of the North-African Houbara bustard compatible with the persistence of sustainable traditional falconry (recognised as a human living heritage by UNESCO, <https://ich.unesco.org/en/RL/falconry-a-living-human-heritage-01209?RL=01209>). The ECWP conservation strategy combines *ex* and *in-situ* actions: 1) establishment of a sustainable conservation breeding, 2) production in captivity of Houbara for reinforcement able to survive and breed successfully in the wild, 3) release of numbers in accordance with hunting yields to stop the population decline and allow regulated falconry, 4) protection of reinforced population. Even though survival and reproduction of captive-bred released individuals in the wild has a relevant impact on the persistence of the population, our simulations indicates that at this stage and from a conservative point of view (Robert et al. 2015a, 2015b, Seddon et al. 2014), the reinforcement programme cannot be considered as a success. Indeed, without the maintenance of translocation interventions the population is not viable on the long-term, as observed in other species and translocation programmes (see e.g. Martínez-Abrain et al. 2010). From such finding one would argue that the stoppage of hunting would be the only valuable action for the restoration of the North-African Houbara bustard, as proposed for other bustard species (Burnside et al. 2016). Interestingly, our results underline that the population remains vulnerable to extinction even if hunting ceased. These results all together emphasise the importance of other environmental factors than hunting on Houbara life parameters that remain to be assessed (climate change, human disturbance, habitat degradation, translocation strategies etc.). Future fundamental and applied researches of the ECWP should aim at evaluating the relative impact of these factors on population demographics. Such assessments are keys to improve *in situ* measures (e.g., habitat protection or restoration, limitation of human disturbance, etc.) and fine-tune the current conservation strategy (e.g., testing alternatives hunting management and protection scenarios), including modifying the reinforcement strategy (e.g., decreasing release effort within protected areas to limit density dependent effects, Azar et al. 2016, Monnet 2014). Such adaptive management

scheme requires long term researches and experiments that can't be achieved without the full support of all stakeholders, especially local authorities, hunters (falconers) and human local populations. The reinforcement for hunting and conservation are thus two non-dissociable components of the strategy which allowed stopping population decline while re-establishing falconry. This pragmatic approach provides a mandatory timeout and financial support to build and improve future conservation strategy.

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Supplementary materials – Article 4

Appendix A. Breeding stations of the Emirates center for Wildlife Propagation (ECWP)

ECWP is organized into a network of specialized stations: two breeding stations and four rearing stations where future releases are prepared for reinforcement. The two breeding stations, Missouri station created in 1995 and Enjil Station created in 2005, respectively hold 3 500 and 6 000 breeders, all kept in individual cages. All eggs produced through the artificial reproduction process are incubated at Missouri station in an incubation building of a full capacity of 40 000 eggs. The annual production capacity is 20 000 birds and all stations together can shelter 30 000 birds (breeders and production).

Appendix B. Number of captive-bred Houbaras released per year in the Eastern intervention area of the ECWP

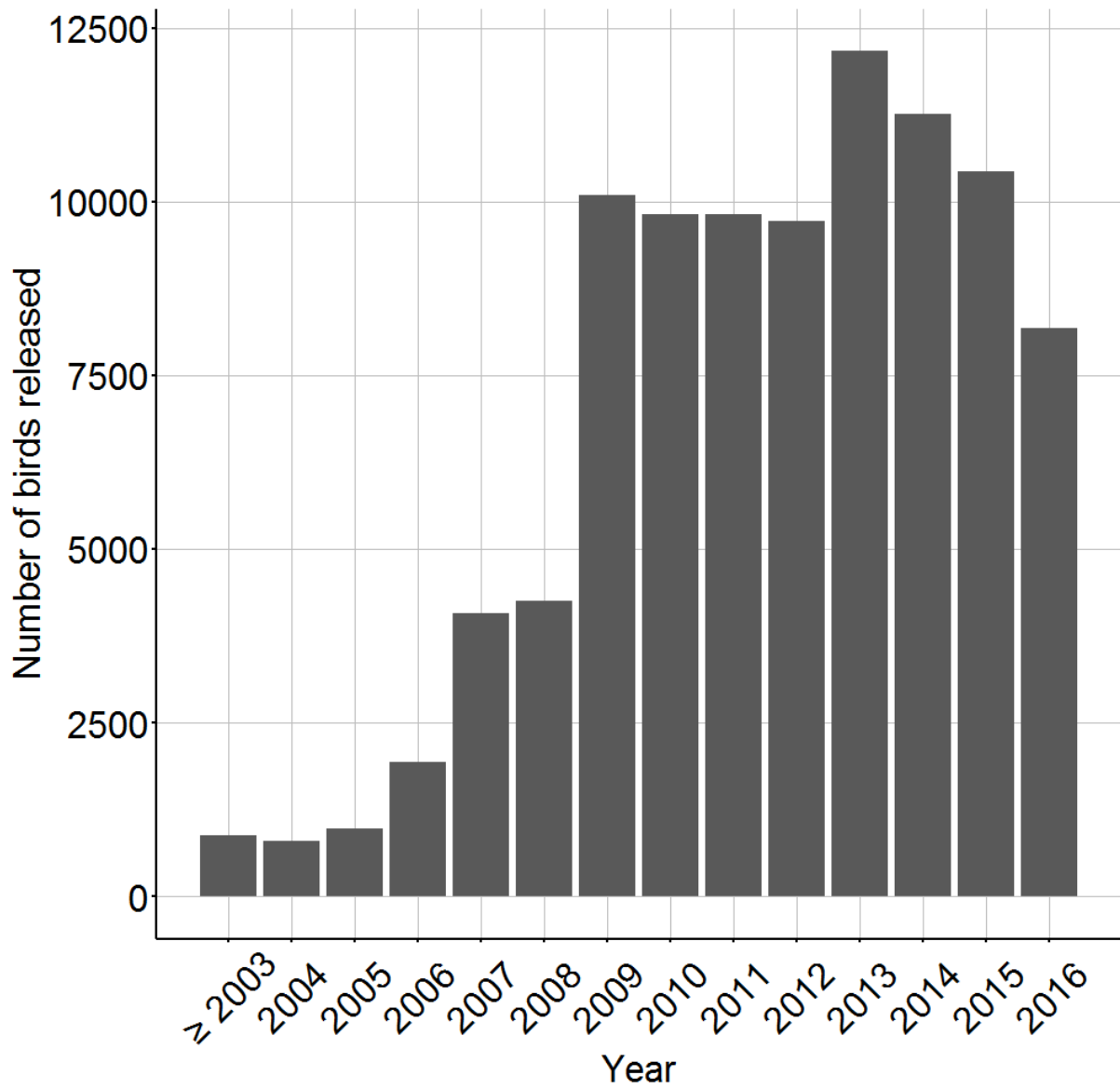


Figure B. Number of captive-bred Houbaras released per year in the Eastern intervention area of the ECWP

Appendix C. Leslie matrix for the deterministic model

Table C. Leslie matrix for the deterministic model

	Juvenile	1	2	3	4	5	6	7	8	9	10	11	12	13
Juvenile	0.00	0.02	0.10	0.25	0.28	0.29	0.29	0.30	0.29	0.28	0.28	0.28	0.28	0.00
1	0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	0.00	0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	0.00	0.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	0.00	0.00	0.00	0.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5	0.00	0.00	0.00	0.00	0.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.00	0.00	0.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7	0.00	0.00	0.00	0.00	0.00	0.00	0.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.89	0.00	0.00	0.00	0.00	0.00	0.00
9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.89	0.00	0.00	0.00	0.00	0.00
10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.89	0.00	0.00	0.00	0.00
11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.89	0.00	0.00	0.00
12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.89	0.00	0.00
13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.89	0.00

Appendix D. Minimum and maximum annual survival and productivity values of the Houbara in Eastern Morocco.

Table D.1. Minimum and maximum estimated annual survival rates of the Houbara in Eastern Morocco.

Extreme values	Survival Individuals ≥ 2 years old
Survival Min (2012)	0.54
Survival Max (2005)	0.97

Table D.2. Minimum and maximum age dependent annual productivity of the Houbara in Eastern Morocco.

Extreme values	Age										
	1	2	3	4	5	6	7	8	9	10-13	
Productivity Min (2011)	0.00	0.02	0.03	0.10	0.14	0.19	0.24	0.29	0.28	0.27	
Productivity Max (2009)	0.03	0.25	0.35	0.79	0.85	0.90	0.94	0.96	0.94	0.91	

Appendix E. Fate diagram for Houbara dispersal calculation

Houbara dispersal probabilities from hunting to non-hunting and non-hunting to hunting areas were calculated based on Hardouin et al. (2015)'s results and fate diagram calculation.

Within Hardouin et al. (2015) dispersal probability between areas was dependent on the sex and the time after release (short term dispersal probability was considered for the first 6

months after releases, and long-term dispersal was considered for 6 months intervals after short-term dispersal). Therefore we calculated dispersal for one year old individuals and 2 years and older individuals. We assumed wild-born juveniles were not dispersing. Yearly dispersal was calculated as the sum of two 6 months dispersal probabilities (fig E.1, E.2).

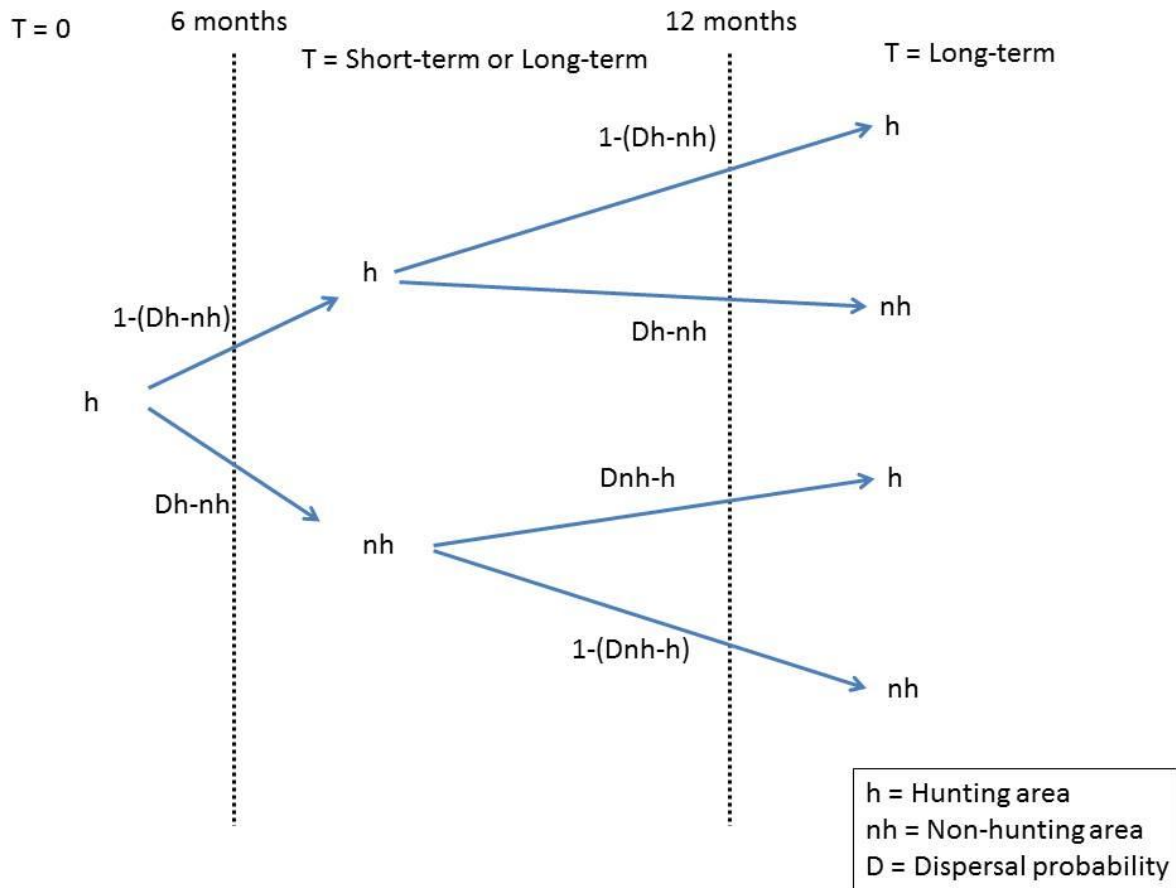


Figure E.1. Fate diagram for calculating Houbara dispersal probabilities from hunting to non-hunting areas.

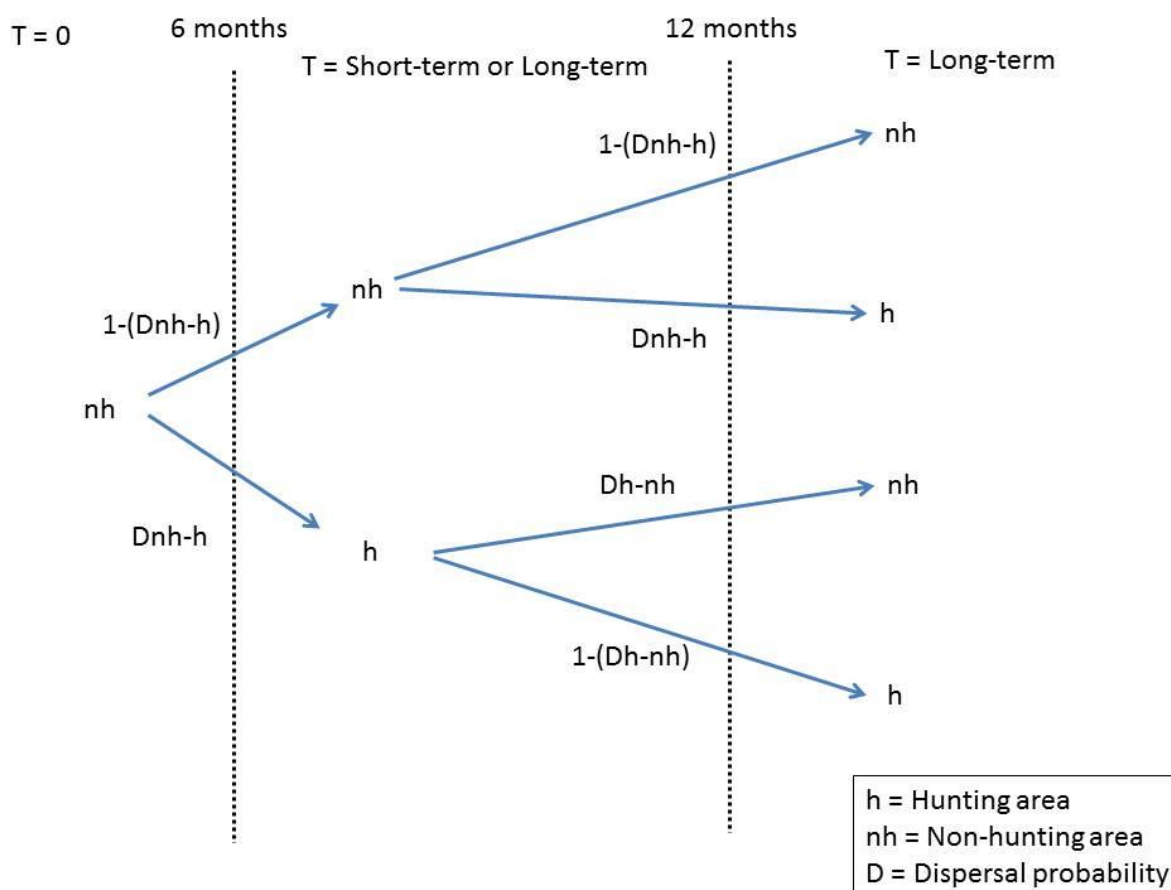


Figure E.2. Fate diagram for calculating Houbara dispersal probabilities from non-hunting to hunting areas.

Appendix F. Houbara population size estimate in non-hunting and hunting area within the Eastern intervention area between 2001 and 2016.

Population size estimates are based on autumnal counts of Houbara bustards using point transects and distance sampling analysis (Thomas et al. 2010). Densities are estimated per 2.5 arc-minutes grid and abundance are then extrapolated to the entire intervention area.

Table F. Estimated populations size of Houbara in the ECWP Eastern intervention area (and compartmented between hunting and non-hunting areas) from 2001 to 2016.

Area	2001-2003	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Non-hunting	808	6920	5243	11553	10432	7859	3789	3027	2881	5990	4413
Hunting	2030	17628	13387	28865	24966	18985	9502	7616	7253	15089	11039
Eastern area	2838	24548	18630	40419	35397	26844	13291	10643	10134	21079	15452

Appendix G. Houbara hunting bags individual identification

During the hunting seasons 2014/2015 to 2016/2017, members of the ECWP were commissioned to report Houbara hunting bags and identify hunted birds for part of the hunting sessions. Captive-bred individuals were identified from their tags (band or transponder). Birds with no tags were assumed to be born in the wild.

Table G. Number of wild-born and captive-bred Houbara hunted

Hunting season	Wild-born	Age of captive-bred females													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
2016/2017	70	79	233	212	61	29	8	11	19	14	1	0	0	0	0
2015/2016	162	98	282	88	31	21	13	7	8	1	0	0	0	1	0
2014/2015	18	62	103	37	10	10	5	3	2	1	0	1	0	0	3

Appendix H. Elasticities results for every Houbara life-history parameters of the deterministic model

Table H. Rounded elasticity values for the Houbara life history parameters from the Leslie matrix.

	Juvenile	1	2	3	4	5	6	7	8	9	10	11	12	13
Juvenile	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
1	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12
2	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00
9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00
10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00
11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00
12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

References in supplementary materials

- Hardouin, L.A., Hingrat, Y., Nevoux, M., Lacroix, F., Robert, A., 2015. Survival and movement of translocated houbara bustards in a mixed conservation area. *Animal Conservation* 18, 461–470. doi:10.1111/acv.12196
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*Chapitre 4. Renforcement, protection et gestion cynégétique de l'outarde Houbara nord-africaine :
une évaluation de la dynamique de la population*

Conclusion et perspectives

Le programme de renforcement de la population exploitée d'outarde Houbara nord-africaine vise à l'établissement d'une population stable et viable, compatible avec le maintien d'activités de chasse traditionnelle. Dans ce cadre, l'ECWP se base sur une stratégie qui combine des actions *in et ex situ* :

- 1- L'établissement d'un élevage conservatoire durable
- 2- La production en captivité d'individus pour le renforcement, capables de survivre et de se reproduire en milieu naturel
- 3- Des lâchers d'oiseaux pour freiner le déclin de la population et répondre à la demande de chasse
- 4- La protection de la population renforcée

A travers cette thèse nous nous sommes intéressé au second axe, en tentant d'évaluer les paramètres de reproduction des outardes Houbara en milieu naturel, de comprendre quels facteurs environnementaux et individuels affectent leurs performances et de quantifier l'apport des renforcements à la dynamique de la population. L'objectif final et appliqué de cette thèse est le développement de modèles quantitatifs de viabilité des populations pour évaluer le programme de renforcement. Cependant, cette finalité repose en amont sur la collecte de données et l'étude des paramètres de reproduction, qui rassemblent la quasi-totalité de l'effort de travail de cette thèse. Dans la mesure où le programme de renforcement se base sur des individus produits en captivité, nous avons cherché dans un premier temps à évaluer les performances reproductrices des femelles lâchées.

Performances reproductrices et caractéristiques individuelles

Le succès d'un programme de translocation nécessite, avant toute chose, que les individus issus des translocations survivent et se reproduisent (Bertolero & Oro 2009, Ewen et al. 2012). Bertolero & Oro (2009) ont montré que les difficultés de réintroduction de l'émyde lépreuse (*Mauremys leprosa*) dans le delta d'Ebre en Espagne étaient en partie liées à la quasi-absence de reproduction chez les individus réintroduits. Dans le cas de la population renforcée d'outarde Houbara, le suivi de la population reproductrice a permis de montrer que les mâles (Cornec et al. 2014, ECWP données non publiées) et femelles (la présente thèse)

lâchés ont des comportements reproducteurs (respectivement parades sur des leks et initiation de nids).

Les femelles lâchées présentent une productivité non nulle, amenant des poussins jusqu'à l'envol. Elles contribuent ainsi à la dynamique de la population au-delà de leur histoire de vie individuelle. De plus, les suivis d'individus reproducteurs sur plusieurs années ont montré que les individus lâchés participent à la reproduction de manière régulière et sur le long terme, suivant un patron de maturation sexuelle puis de sénescence en adéquation avec les patrons observés chez les oiseaux en milieu sauvage (e.g., Jones et al. 2008). Ce patron âge-dépendant observé à la fois en captivité (Preston et al. 2015) et en milieu naturel souligne le maintien de processus éco-évolutif chez les individus produits en captivité et lâchés dans la nature.

Comparées à d'autres populations d'Otididae, telles que celles de la grande outarde en Espagne (*Otis tarda*, Morales et al. 2002), de l'outarde canepetière en France (*Tetrax tetrax*, Inchausti & Bretagnolle 2005) ou une population réintroduite d'outarde de Macqueen aux Emirats Arabes Unis (Azar et al. 2017), les performances reproductrices et la productivité des outardes Houbara lâchées semblent similaires voire supérieures. Toutefois, les performances reproductrices au long terme des individus lâchés se sont montrées en partie inférieures à celles d'individus nés à l'état sauvage, selon leur période de lâcher. Ce coût au lâcher dépendant de la période de lâcher a aussi été observé sur la survie à court terme après le lâcher des individus (Hardouin et al. 2014).

Une explication possible pour les patrons de coût observés pour la reproduction est que la forte mortalité des oiseaux lâchés à court terme s'accompagne d'une modification des performances reproductrices moyennes de la population « survivante ». Ce phénomène est attendu si les performances de survie et de reproduction des individus covarient positivement (e.g., « fixed heterogeneity », Cam et al. 2016). Pour mieux comprendre la cause de ces coûts au lâcher, la poursuite des études de l'hétérogénéité démographique devrait se focaliser sur l'évaluation de ces covariations, qui pourraient expliquer les différences de performances reproductrices entre les femelles lâchées à l'automne et au printemps. Le nombre important d'oiseaux suivis avec des émetteurs pourrait permettre d'explorer comment survie et performances reproductrices co-varient en fonction de l'âge des femelles. De plus, la mise en place du protocole d'identification des femelles au nid avec lecteurs RFID permettra, d'ici quelques années, d'obtenir des histoires de capture suffisamment conséquentes pour calculer

des survies annuelles de femelles reproductrices pouvant être reliées à leurs performances reproductrices.

Nos recherches sur l'expression individuelle des paramètres de reproduction se sont arrêtées à une description phénotypique de celle-ci. Il serait maintenant nécessaire d'examiner la base génétique des paramètres de reproduction en milieu naturel. En se basant sur le pedigree complet des individus produits en captivité, il serait possible d'utiliser des « Animal Model », de quantifier la part de variance génétique additive dans l'expression des caractères et de voir dans quelle mesure ceux-ci sont héréditaires (Kruuk 2003, Merilä and Sheldon 2000). La caractérisation de la base génétique dans l'expression des paramètres de reproduction des individus lâchés produits en captivité représente un axe de recherche de premier ordre. Elle permettra de mieux appréhender les risques génétiques liés à la production d'individus en captivité (risques de sélection et d'adaptation génétique au milieu captif, Chargé et al. 2014) et aux objectifs de renforcement pour l'intégration d'individus à la population reproductrice sauvage (risques d'introgession génétique dans la population sauvage).

Influences environnementales

Dans l'ensemble des analyses, nous avons travaillé sur des tailles d'échantillons importantes pour plus de robustesse statistique et embrasser au mieux la variabilité individuelle. Une conséquence majeure de ce choix est l'étendue importante de la population étudiée (Oriental marocain, 50 000 km²). A cette échelle, il a été difficile de disposer de données environnementales précises pour chaque femelle suivie, chaque nid ou chaque poussin, comme l'habitat des sites de reproduction, l'activité anthropique (Koshkin et al. 2016) ou les données météorologiques locales. Malgré cela, à l'échelle régionale, nous avons mis en évidence l'influence positive de fortes précipitations hivernales sur les performances reproductrices (survie des nids et taille de couvée) des outardes Houbara lâchées. Dans les milieux désertiques, la production primaire et secondaire annuelle est largement influencée par les niveaux de précipitations (Gamoun 2016). Ainsi, une plus grande abondance et disponibilité des ressources pourraient favoriser l'investissement reproducteur des femelles. Dans la continuité de ces résultats, il serait intéressant d'étudier comment les fluctuations météorologiques passées peuvent influencer la démographie de la population. Les fluctuations météorologiques en milieu désertiques et les phénomènes d'accumulation peuvent avoir des effets à retardement de plusieurs années sur la productivité du milieu (Reichmann et al. 2013, Sala et al. 2012). L'accumulation de fortes précipitations ou de périodes de sécheresse sur

plusieurs années consécutives pourrait conduire à des réponses démographiques de la population très différentes de celles pouvant être observées à la suite de pics de précipitation ou de sécheresse occasionnelle.

Au niveau intra-annuel, nos recherches ont souligné une diminution des performances reproductrices au cours de la saison de reproduction. Nous n'avons pas été en mesure de quantifier l'importance des facteurs liés à l'hétérogénéité démographique (individus moins performants qui initient leur nid plus tard) et l'hétérogénéité environnementale (conditions environnementales moins favorables en fin de saison de reproduction) (Grüebler et Naef-Daenzer 2010). Il est maintenant nécessaire de se focaliser sur le déliement des facteurs qui jouent sur ce déclin. L'étude des paramètres de reproduction avec l'avancement de la saison a permis par ailleurs de mettre en évidence un lien dynamique entre survie des nids et indice de qualité d'habitat qui pourrait être expliqué par une dynamique des conditions environnementales et processus écologiques au cours de la saison de reproduction. Ce résultat a montré, avant tout, la complexité de caractériser la qualité d'un habitat, du fait de la dynamique des processus écologiques qui s'y déroulent. De plus, il laisse à penser que les modèles de niche développés à l'heure actuelle devraient être utilisés avec prudence pour guider les actions de conservation et translocation, car ils ne sont pas forcément indicateurs d'habitats stables et favorables, au moins concernant la survie des nids, pour l'outarde Houbara. Les causes de ce lien dynamique ne sont que des suppositions et il serait nécessaire de s'intéresser directement à la caractérisation des interactions biotiques, notamment aux processus de compétitions et perturbations intra et inter-spécifiques, sur les performances reproductrices, et à leur dynamique au cours de la saison de reproduction. L'étude des interactions intra-spécifiques permettrait notamment d'envisager les mécanismes liés aux importants efforts de lâcher et fortes densités d'oiseaux, qui peuvent avoir des effets délétères sur les performances démographiques individuelles et la viabilité de la population (Azar et al. 2016).

Dans le cas de la population étudiée, qui reçoit des renforcements importants et fréquents, la question de l'influence des densités et de leurs variations dans le temps et l'espace est de premier ordre. Azar et al. (2016) ont montré, dans une population réintroduite d'outarde de Macqueen, que la survie à long terme des individus était négativement affectée par des lâchers ultérieurs d'individus. Ceci serait lié à l'augmentation locale des densités d'outardes provoquant des processus densité-dépendants. Chaque année, des comptages sont effectués à l'automne pour estimer les densités d'outardes Houbara dans les aires d'intervention. Mais les

aires d'intervention de l'ECWP sont très étendues et malheureusement, une estimation annuelle des densités locales selon des gradients spatiaux semblent difficilement atteignable. Face à cette limite, le développement de protocoles expérimentaux s'appuyant sur le programme de renforcement semble être une solution pertinente. Cela pourrait se faire en définissant des parcelles, pendant la saison de reproduction et avec des standards de qualité d'habitat et de gestion, dans lesquelles différents effectifs d'oiseaux seraient lâchés. Il serait alors possible de mesurer comment densités locales et interactions intra-spécifiques affectent les performances démographiques des individus reproducteurs.

D'un point de vu inter-spécifique, des recherches devraient se développer sur la caractérisation spatiale et temporelle des prédateurs d'outardes. Les suivis de nids par pièges photographiques ont montré une forte proportion d'échecs causés par la prédation des œufs (au moins 74% des échecs de nids causés par de la prédation). Cette prédation pourrait avoir une influence majeure sur la productivité totale de la population. Une exploitation approfondie des données de pièges photographiques (événements de prédation au nid) permettrait d'obtenir des fréquences d'évènements de prédation, desquels il serait possible de caractériser au niveau temporel et spatial des abondances relatives de prédateurs (O'Connell et al. 2011). En les reliant à des données météorologiques, nous pourrions alors mieux comprendre les mécanismes qui jouent sur les performances reproductrices des outardes.

La zone d'étude d'al Baten se présente comme un site d'étude idéal pour développer ces questions d'influences locales de l'environnement (Fig. 27). Il s'agit d'une aire de réserve où la population de mâles reproducteurs est suivie annuellement depuis 2005. Une nouvelle cartographie précise des habitats est disponible depuis 2017, accompagnée d'un suivi systématique des ressources trophiques pour les outardes. De plus, cette zone fait l'objet d'un suivi des activités anthropiques (activités pastorales et agricoles) qui pourraient être utilisées pour en mesurer les impacts sur les populations reproductrices (Koshkin et al. 2016, Le Cuziat et al. 2005). Cependant l'étude de l'influence de facteurs environnementaux à l'échelle locale reste difficile à mettre en œuvre car les outardes Houbara femelles ne présentent pas de fidélité systématique à un site de nidification et pourraient sélectionner leur site selon les disponibilités et perturbations de l'habitat (Hingrat et al. 2007a, Le Cuziat et al. 2005), ce qui limite la définition d'une zone d'étude dédiée sur un pas de temps interannuel.

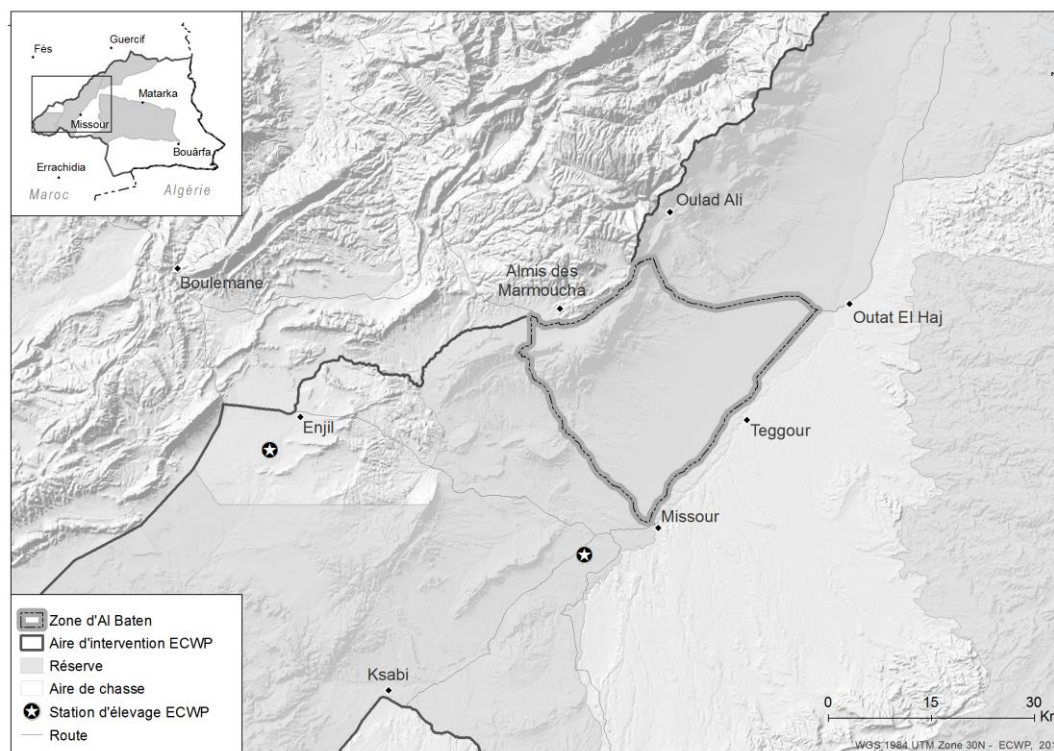


Figure 27. Localisation de la zone d'al Baten dans l'aire d'intervention ECWP de l'Oriental.

Apports au programme de renforcement de l'ECWP

L'étude des paramètres de reproduction a permis, dans un premier temps, de montrer que les individus lâchés produits en captivité s'intègrent à la population reproductrice en milieu naturel. L'identification de coûts au lâcher et leurs variations en fonction des stratégies de gestion offre l'opportunité d'améliorer les performances reproductrices moyennes au sein de la population, en favorisant par exemple les lâchers d'automne. Néanmoins, même si les lâchers d'automne présentent un avantage démographique, et possiblement conservatoire, il est nécessaire de prendre en compte les aspects cynégétiques dans le renforcement des populations. Ainsi les lâchers de printemps présentent toujours un avantage, car ils permettent de maintenir la population à un niveau élevé et pourraient donc absorber en partie la pression de chasse, protégeant ainsi la population reproductrice effective.

Finalement, la détermination de la productivité individuelle nous a permis de compléter les indicateurs démographiques nécessaires au développement de modèles quantitatifs de viabilité des populations. Les résultats présentés dans le chapitre 4 ne sont que préliminaires. Les calculs de dynamique de population et de risque d'extinction sont basés sur un nombre faible de trajectoires ($n=100$), pour des raisons liées au temps de calcul. Ces calculs seront affinés sur la base d'un nombre plus important d'itérations ($n=1000$). Même si la survie et la

reproduction des individus lâchés ont un impact sur la persistance de la population renforcée, nos simulations indiquent que dans l'état actuel et d'un point de vu conservatoire, le programme de renforcement ne peut pas être considéré comme un succès (Robert et al. 2015a, Seddon et al. 2014). Le programme de renforcement de l'ECWP se trouve à l'interface entre actions conservatoires et intérêts cynégétiques. La création du programme a été motivée, au moins en partie, par le maintien d'une activité de chasse traditionnelle au faucon. Nous nous trouvons donc dans un cas particulier où les objectifs conservatoires et critères scientifiques établis pour évaluer un programme de translocation peuvent ne pas être pertinents. A l'inverse, présenter l'ECWP selon des motivations et intérêts purement cynégétique en font un programme de renforcement singulier, voire exemplaire face à d'autres programmes de renforcement à visée cynégétique. De nombreux programmes de renforcement de populations exploitées ne suivent pas les directives IUCN concernant l'élevage et la translocation d'individus, malgré les risques pour les populations sauvages (Barbanera et al. 2010, Champagnon et al. 2013). L'ECWP vise à respecter au mieux les directives de l'IUCN, dans un souci d'intégrité écologique et génétique de la population sauvage et de son écosystème.

Les modèles développés ont montré que, même dans l'hypothèse d'un arrêt de la chasse, la population reste vulnérable. Ce résultat souligne l'importance d'autres facteurs que la chasse sur la persistance de la population (changement globaux, dégradation de l'habitat, stratégies de translocation etc.). A l'avenir, les objectifs de recherches fondamentales et appliquées de l'ECWP devraient se focaliser sur l'évaluation de l'impact de ces facteurs sur la démographie de la population. Ces recherches permettront d'améliorer les mesures de conservation *in situ* (protection et restauration de l'habitat, limitation des perturbations anthropiques), d'améliorer les stratégies de translocations (e.g. diminution de l'effort de renforcement pour diminuer des effets densités dépendants, Azar et al. 2016, Monnet 2014) et de protections (e.g. définition de nouvelles méthodes de protection et de chasse). Un tel système de gestion adaptative (Armstrong & Seddon 2008) nécessite des programmes de recherche et des expériences au long terme, au profit de la conservation et de la science en général, mais ne peut être réalisé sans le plein soutien de toutes les parties prenantes, en particulier les autorités locales, les chasseurs (fauconniers) et les populations locales humaines. Au final, les actions de renforcement pour la chasse et la conservation de la population apparaissent comme deux éléments non dissociables d'une stratégie globale qui ont permis d'arrêter le déclin de la population tout en rétablissant la fauconnerie.

Conclusion et perspectives

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Annexes

Annexe 1. Effets des outils de suivis (Pièges photographiques, émetteurs et lecteurs RFID) sur le taux de survie journalier des nids.

En se basant sur le jeu de données et la méthode d'analyse statistique de l'article 1, nous avons voulu évaluer si les différents outils appliqués au suivi des nids et à l'identification des femelles affectaient le taux de survie journalier des nids. Pour chaque intervalle de visites de chaque nid, nous avons indiqué si :

- oui (1) ou non (0) la femelle était équipée d'un émetteur (Emetteur)
- oui (1) ou non (0) le nid était équipé d'un piège photographique (Présence piège photographique)
- oui (1) ou non (0) il y a eu déploiement d'un lecteur RFID lors de la visite qui initie l'intervalle (Présence lecteur RFID)

En se basant sur la méthode d'inférence multi-modèles de l'article 1, nous avons développé l'ensemble des modèles candidats incluant les différentes combinaisons des effets additifs des covariables, effets quadratiques, interactions (voir étape 2, « second step ») et effets additifs des variables binaires (0-1) « Emetteur », « Présence piège photographique » et « Présence lecteur RFID ». L'année et l'identité des femelles aux nids étaient incorporées en effets aléatoires dans tous les modèles. Nous avons ensuite estimé les coefficients moyennés des effets sélectionnés dans les meilleurs modèles ($\Delta AICc < 2$). Pour plus de détails sur l'approche statistique voir article 1.

Les trois variables binaires sont présentes dans au moins 1 des meilleurs modèles. Seule la présence d'émetteur affecte significativement le taux de survie journalier des nids (tableau A1).

Annexes

Tableau A1. Coefficients moyennés des variables sélectionnées dans l'ensemble de meilleurs modèles ($\Delta AICc < 2$) pour les analyses de taux de survie journalier des nids.

Variabiles	Coefficient	IC-	IC+	Importance relative
Age du nid	-0.94	-1.18	-0.70	1
Age du nid ²	-0.07	-0.45	0.30	0.29
Date d'initiation du nid	-0.21	-0.43	0.00	0.79
Précipitations hivernale	0.38	0.12	0.64	0.95
Températures hivernale	-0.18	-0.42	0.07	0.61
Age de la femelle	0.09	-0.14	0.33	0.77
Age de la femelle * Températures hivernale	-0.29	-0.70	0.13	0.26
Présence piège photographique	-0.05	-0.30	0.20	0.28
Emetteur	-0.42	-0.65	-0.18	0.99
Présence lecteur RFID	-0.14	-0.41	0.14	0.37

IC- = Valeur basse de l'intervalle de confiance à 95%, IC+ = Valeur haute de l'intervalle de confiance à 95%,
 Importance relative = somme des poids d'AICc des modèles où la variable est présente.

Annexe 2. Choix de la méthode d'analyse pour l'article 2.

Contrairement aux analyses des articles 1 et 3, où les résultats sont basés sur les coefficients moyennés d'un ensemble de modèles sélectionnés ($\Delta AIC_c < 2$, Burnham & Anderson 2002), les résultats de l'article 2 se basent sur les coefficients estimés du « meilleur » modèle ($\Delta AIC_c = 0$).

Le calcul des coefficients moyennés d'un ensemble de modèles pour évaluer les effets de variables est une technique à utiliser avec prudence lorsque des termes supérieurs (effets d'interaction ou polynômes), liés à des effets additifs, sont présents (Banner & Higgs 2017). Dans un modèle incluant uniquement des effets additifs, les coefficients des variables sont indépendants, alors que dans un modèle incluant des interactions, l'effet additif d'une variable spécifique dépend de la variable avec laquelle il interagit.

Si la moyenne des coefficients d'une variable se base sur des modèles incluant l'effet additif de la variable considérée et des modèles incluant l'effet additif et son interaction avec une autre variable, alors la moyenne des coefficients des effets additifs sera faussée. Par conséquent, pour les articles 1 et 3 nous avons compartimenté nos analyses en deux étapes (voir méthodes article 1). La seule condition de validité de cette procédure est que, dans la seconde étape, seuls les coefficients moyens des interactions, des termes quadratiques (les termes supérieurs dans notre cas) et coefficient moyens des effets additifs qui n'interagissent pas sont pertinents à interpréter.

Dans l'article 2, pour chaque paramètre de reproduction étudié, les coefficients estimés des variables sélectionnées dans le meilleur modèle ($\Delta AIC_c = 0$) montrent les mêmes tendances et significativités que les coefficients moyennés basés sur un ensemble de modèles ($\Delta AIC_c < 2$, voir tableau A2 ci-dessous. Le tableau A2 a été laissé en anglais pour pouvoir être comparé à celui de l'article 2). Pour chaque paramètre de reproduction étudié, les coefficients moyennés (effets additifs et interactions) des variables non-sélectionnées dans le meilleur modèle ne sont pas significativement différents de zéro (voir tableau A2), quel que soit le niveau de référence choisi en ordonnée à l'origine pour « Female origin » (pour les effets de variables catégorielles, les résultats présentent les différences par rapport à un niveau de référence en ordonnée à l'origine. Dans le tableau A2, le niveau de référence est « Wild-born females », mais nous avons examiné les différences pour chaque niveau « Female origin » en ordonnée à l'origine). Nous avons donc décidé de prendre en compte uniquement le meilleur modèle et

de ne pas considérer les coefficients moyennés dans la présentation des résultats de l'article 2. Les méthodes du second article étant conséquentes (capture et identification des individus nés à l'état sauvage, prise en compte des biais inhérent à la capture d'individus, etc.), ce choix nous a permis d'alléger son contenu et de garder plus de clarté dans les résultats.

Tableau A2. Coefficients moyennés (\pm 95% IC) des variables sélectionnées pour les deux ensembles de modèles ($\Delta AIC_c < 2$) d'analyses de chaque paramètre de reproduction. 1. La première étape se focalise sur les effets additifs. 2. La deuxième étape se focalise sur les effets additifs, quadratiques et interaction.

Variables	Nesting effort	Nest date	initiation	Clutch size	Egg volume	DNSR	DBSR
1. Additive effects (first set of candidate models)							
Carry-over trapping	-	-	-	0.09 [-0.44 ; 0.63]	0.06 [-0.95 ; 1.06]	0.09 [-0.34 ; 0.52]	-0.39 [-1.16 ; 0.38]
Direct trapping	-	-	-	-	-	-	-1.83 [-2.74 ; -0.93]
Date	-	-	-	-0.97 [-1.35 ; -0.59]	-1.60 [-2.20 ; -1.00]	-0.17 [-0.44 ; 0.10]	0.30 [-0.11 ; 0.72]
Brood age	-	-	-	-	-	-	0.67 [0.15 ; 1.19]
Nest stage	-	-	-	-	-	-2.51 [-4.48 ; -0.55]	-
Female origin (Intercept = Wild-born):				Not selected		Not selected	
Released in autumn	-0.47 [-0.99 ; 0.05]	4.69 [-2.34 ; 11.72]			-0.80 [-2.48 ; 0.89]		0.08 [-0.58 ; 0.74]
Released in spring	-0.64 [-1.16 ; -0.13]	3.90 [-1.87 ; 9.66]			-1.71 [-3.12 ; -0.31]		-0.51 [-1.01 ; -0.01]
Female's age	1.74 [1.10 ; 2.37]	-11.27 [-17.83 ; -4.70]		1.01 [0.47 ; 1.55]	4.14 [2.76 ; 5.51]	0.10 [-0.29 ; 0.49]	1.11 [0.44 ; 1.77]
2. Additive and interaction effects (second set of candidate models)							
Female's age							
*Origin(Intercept = Wild-born):	Not selected	Not selected		Not selected		Not selected	
Female's age * Released in autumn					1.20 [-2.61 ; 5.00]		1.21 [-0.72 ; 3.15]
Female's age * Released in spring					3.53 [-0.51 ; 7.56]		1.33 [-0.52 ; 3.17]
Date ²	-	-		-0.42 [-1.00 ; 0.17]	0.11 [-0.77 ; 0.98]	Not selected	-0.35 [-0.86 ; 0.16]
Brood age ²							-0.12 [-1.14 ; 0.90]

"Not selected" indicates that the covariate was not selected in the best set of models and "-" indicates that the covariate was not included in the global model. DNSR = Daily Nest Survival Rate, DBSR = Daily Brood Survival Rate. For binary factor Carry-over trapping : Not consecutive to trapping = 0, Carry-over trapping = 1. For binary factor Direct trapping: No trapping = 0, Trapping of brooding female = 1. For binary factor Nest stage: Laying stage = 0, Incubation stage = 1. For binary factor Female's age: One year old females = 0, Two years and older females = 1. Coefficients are in bold, where 95% CIs do not include zero.

Référence - Annexe 2

Banner, K.M., Higgs, M.D., 2017. Considerations for assessing model averaging of regression coefficients. *Ecological Applications* 27, 78–93. doi:10.1002/eap.1419

Annexes

