Conservation of a very rare species in a rapidly changing context:

Cambodia’s Bengal Florican

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Abstract

The Southeast Asian subspecies of Bengal Florican *Houbaraopsis bengalensis* *blandini*, a Critically Endangered bustard, is one of the most threatened bird taxa in Southeast Asia. The only remaining population is located in the Tonle Sap Floodplain, Cambodia. This thesis consists of research that addresses the question of how can a species that is so poorly adapted to the modern world be saved from extinction in the context of a country undergoing rapid development and change? I first quantify the recent rapid population decline and show that Bengal Florican abandon sites when suitable habitat contracts to less than 25 km². I show that conservation measures have stabilised the population at one small site, and I evaluate progress in research and management from that site, and from sites in India and Nepal that support florican populations, and use these to develop a framework for conservation collaboration across sites. I then build a case for immediate conservation action by showing that recent habitat changes in the Tonle Sap Floodplain due to agricultural intensification in Cambodia are greater than the predicted future impacts of climate-change and hydropower dams. However, because *in situ* conservation alone may be insufficient to save *H. b. blandini*, I apply the IUCN guidelines for captive management and use a decision tree to help stakeholders thoroughly consider the risks associated with *ex situ* conservation. Lastly, I draw on my experience of Bengal Florican conservation to propose a theory, called the law of small sites, to explain why small sites, such as those used by remaining floricans, are of high importance for conservation; I also explain why the nature of this explanation is important for the conservation of very rare species. I conclude by discussing my research in the context of how success in conservation of *H. b. blandini* could be conceptualised.
Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. I give consent to this copy of my thesis, when deposited in the University Library, being made available for loan and photocopying online via the University's Open Access repository eSpace.

Simon P. Mahood

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Publications and Author Contributions

Publication 1.


Author contributions: SPM designed and wrote the paper, led and contributed to the data collection, and analysed the data; SV collected data; all co-authors reviewed and provided valuable input to the paper.

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Author contributions: SPM conceptualised and wrote the paper; MJB led the data analysis, JBS developed Figure 1, all co-authors reviewed and provided valuable input to the paper.
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Chapter 1. Introduction

1.1 Introduction

The world is changing faster than at any time in recorded history, with people the cause of that change (Watson et al. 2018). We have the technology, and we are so great in number, that we are changing the climate, destroying ecosystems and causing species extinctions (Butchart et al. 2010; Dirzo et al. 2014). A growing awareness of our impacts on nature, and of the importance of the services that nature provides to people, has led to a global conservation movement one of whose missions is to prevent extinctions (CBD 2010; Godet & Devictor 2018).

Despite their efforts, the number of species threatened with extinction is increasing (Hoffmann et al. 2010), owing largely to the impacts of habitat loss and degradation for agriculture, and overexploitation (Maxwell et al. 2016). However, there is growing evidence that extinctions can be prevented through judicious use of protected areas, law that prevent hunting and habitat loss, sustainable use of natural resources, habitat restoration and captive management (Hoffmann et al. 2010; Garnett et al. 2018). Because of the scale of human influence on the world, conservation activity takes place both outside and within the remaining wilderness areas (Stokes 2018).
Of species that have been assessed using the IUCN Red List, 27% are globally threatened or Near Threatened; and for birds, the figure is ~14% (Butchart et al. 2004; BirdLife International 2018a). Asia is recognized a global threat hotspot and priority for conservation because it is a center of endemism and has suffered massive habitat loss compounded by heavy trade-driven hunting (Duckworth et al. 2012; Rodrigues et al. 2014). Conservation in Southeast Asia is challenging because most countries are still rich in natural resources, regard their exploitation as a critical step towards development, and sometimes lack the governance necessary to moderate their use (Laurance 2007). The top five countries in the world for human impacts on threatened vertebrates are in Southeast Asia (Allan et al. 2019). This is partly because of the proximity of Southeast Asia to China, which imports exceptionally large volumes of timber, agricultural commodities, minerals and wildlife products from across the world (Hughes 2017). The region has an impressive network of protected areas, but the area covered is below the Aichi 11 target coverage (17%), and it has the greatest shortfall in suitable land to meet that target without restoration (Mappin et al. 2019). Exploitation of timber and clearance of forest for cultivation of commodity crops also impacts protected areas. In Asia, Malaysia and Cambodia stand out because of their high rates of protected forest loss (Spracklen et al. 2015).

Cambodia is a good example of many of these challenges. It is a small (181,035 km²) tropical country with a relatively low human population (16 million) that has recently experienced rapid economic growth, in part fueled by conversion of natural habitats to cash crops such as rice, rubber, sugar and cassava (MAFF 2015). Rates of habitat loss in Cambodia are consequently high, even within a regional context (Hansen et al. 2013). There was a 23% decline in forest cover between 2000 and 2017 (World
Resources Institute 2014), indeed since 1990 Cambodia has experienced one of the
greatest accelerations in deforestation of anywhere in the world (Kim et al. 2015).
Rate of grassland loss is even higher (Packman et al. 2013a). Governance scores are
low, Cambodia is ranked 150 in Transparency International’s corruption perceptions
index (out of 180 countries evaluated), lower than any Asian country other than North
Korea (Transparency International 2017), and most people are poor and depend on
natural resources (Asadullah & Savoia 2018). Since the late 1990’s the Cambodian
ruling political party has consolidated power, and in doing so has created a sufficient
degree of political stability for foreign and national investment (Kelsall & Seiha
2014). Cambodia joined the World Trade Organisation (WTO) in 2004, and the
Association of Southeast Asian Nations (ASEAN) in 2009. Cambodia’s reforms and
development have led to rapid economic growth and a reduction in poverty
(Asadullah & Savoia 2018), but they have come at the expense of habitats and
biodiversity.

Nevertheless, Cambodia still supports populations of Endangered and Critically
Endangered bird species that have been extirpated from neighbouring countries (or
almost so) (BirdLife International 2018a). These include Giant Ibis *Thaumatibis
gigantea* and White-shouldered Ibis *Pseudibis davisoni*, which formerly occurred
across much of mainland Southeast Asia, but now breed only in remote forested
wetlands in the north and east of Cambodia. In the centre of the country is the Tonle
Sap Lake, Southeast Asia’s largest freshwater wetland. Prek Toal, an area of flooded
forest in the floodplain of the Tonle Sap, supports Southeast Asia’s largest waterbird
colony, which contains half of the global population of Greater Adjutant *Leptoptilos
dubius* in their only breeding colony in Southeast Asia (Goes 2013). In the grasslands
and low intensity agriculture in the floodplain of the Tonle Sap Lake is a population
of a Critically Endangered bustard, the Bengal Florican *Houbaropsis bengalensis*
(BirdLife International 2018b). Cambodia is now essential for the conservation of
these species, but it is rapidly developing and the populations of these species are
declining (BirdLife International 2018a).

Those threatened bird species that are found in Cambodia, but have been lost from
elsewhere in Southeast Asia, exhibit many of the characteristics of species with a high
extinction risk. Typically they are large-bodied, at least partially selective for habitat,
require large home-ranges, and have low fecundity (Bennett & Owens 1997; Purvis et
al. 2000). These physical and ecological characteristics make such species not only
especially susceptible to threats, but also inherently more difficult subjects for
conservation efforts.

With the exception of some flightless species, perhaps no group of birds is so
maladapted to the modern world as the bustards, Otididae. The bustards embody all of
the traits that characterize threatened continental species. Of the 26 species of bustard,
eight (31%) are considered globally threatened, with an additional 7 (27%) species
classified as Near Threatened, which makes them one of the most threatened groups
of birds worldwide (BirdLife International 2018a). Asia supports four of the eight
threatened species, indeed all three non-migratory Asian bustard species are Critically
Endangered or Endangered (Collar et al. 2017). One of those Critically Endangered
bustards is the Bengal Florican, which is the only bustard found in Southeast Asia.
The challenge of saving that bustard in its last remaining Southeast Asian population is the subject of this thesis.

1.2 Thesis aims

Conservation of Bengal Florican in Cambodia has reached a crisis point. The aim of this thesis is to answer the question ‘can we save the Bengal Florican in Cambodia, and if so, how?’ I address this question by re-assessing the situation facing Bengal Florican in the light of ongoing and novel threats and evaluating the options that might prevent its extinction. The focus is on Cambodia because that is where the Bengal Florican is in most peril, but wherever possible lessons that are applicable to bustard populations in South Asia are highlighted.

1.3 Thesis layout

The thesis starts with a literature review (Chapter 2), which is divided into three parts. The first part provides historical context on human interactions with bustards and why certain species of bustard are particularly threatened. The second part is an overview of the state of knowledge of Bengal Florican. The last part reviews methods of bustard conservation in Europe, where research and management of bustard populations is most advanced, and evaluates whether there are lessons that could be learned for conservation of Bengal Florican in Cambodia. The data chapters that follow the literature review each make a specific contribution to knowledge of Bengal Florican, or knowledge of Bengal Florican conservation, that aims to answer the question of can Cambodia’s Bengal Florican be saved from extinction.
In Chapter 3, I assess status and trends in Cambodia’s Bengal Florican population since 2012 and evaluate the effectiveness of protected areas that were established to protect it. Up to date knowledge of the status of a taxon is a critical piece of information for making decisions and planning conservation action. In 2013, it was stated that Bengal Florican was declining at such a rate, and had such a low population, that it would be extinct in Cambodia within ten years (Packman et al. 2013b). An update is necessary given the time that has elapsed since that prediction was made, and the rapid changes that have happened in the range of Bengal Florican in Cambodia since that time.

In Chapter 4 I adapt recently published metrics for evaluating conservation progress of bird species (Garnett et al. 2018) to evaluate threats to Bengal Florican sub-populations and assess patterns of progress in research and management across its global distribution. In this chapter I have collaborated with Bengal Florican conservationists from India and Nepal so that we can share knowledge and experience of Bengal Florican status and conservation actions. I use the results of the assessment to develop a new framework for collaboration between Bengal Florican conservationists so that we can maximize the chance of success across sites.

Chapter 5 builds a case for protection of seasonally flooded habitats in the Tonle Sap Floodplain, including the grassland and low intensity agriculture used by Bengal Florican. Much of the conservation discourse around changes in hydrology and
habitats in the Tonle Sap Floodplain revolves around the predicted impacts of hydropower development on the Mekong River and climate change, which are considered future threats (Arias et al. 2012). However, these discussions fail to account for the rapid agricultural intensification of Tonle Sap habitats. In this chapter I redress the situation by evaluating the impact of local-drivers on habitat change in the Tonle Sap Floodplain over the past 25 years, in particular, the proliferation of irrigated agriculture. I show that habitats, including the grassland used by Bengal Florican, are already changing rapidly. I then use historical data on climate and the incidence of fire to show that there are likely to be increased opportunities for people to convert seasonally flooded habitats to agricultural land in the future. I make practical recommendations to mitigate these impacts that would benefit people and Bengal Floricans in the Tonle Sap Floodplain.

Given the parlous state of remaining Bengal Florican populations in Cambodia, I use the IUCN guidelines for *ex-situ* conservation (IUCN/SSC 2014) in Chapter 6 to evaluate whether captive management is appropriate for Cambodia’s Bengal Florican population. There are no published case studies using these guidelines. I concluded that the guidelines would be easier for stakeholders to use were they to have a decision tree to help guide them through the assessment process. The decision tree I developed not only helped answer the question of whether conservation practitioners should start captive breeding of Bengal Florican, but also to frame discussions about the concept of wild and how this might relate to Bengal Florican conservation in the future.
The most important site in Cambodia for the conservation of Bengal Florican is Stoung-Chikreang BFCA, it is not the largest site that supports the species, but it has the largest population and the highest density of Bengal Florican. It is not particularly important for any other species. Chapter 7 is a tribute to the under-appreciated value to conservation of such small sites. In it I propose a novel explanation for why small patches of habitat are frequently the most important places for the conservation of rare species, which I name the Law of Small Sites. This chapter, and the Law of Small Sites, explains why Stoung-Chikreang BFCA came to be so important, and the implications of this explanation for the conservation of all rare species.

Chapter 8 discusses the findings of the preceding chapters and places them in a wider context. In this chapter I discuss the implications of the research for conservation of Bengal Florican in Cambodia, and also for other threatened bustards in Asia. Based on the results of research, I evaluate the critical next steps for conservation of Bengal Florican and evaluate how success might be conceptualized.

Annex 1 contains a paper in which I evaluate how a newly constructed power transmission line might impact Cambodia’s Bengal Florican population. It does not form a part of this thesis.

This thesis includes five data chapters (Chapters 3–7), prepared as manuscripts that have been submitted to peer reviewed scientific journals (as indicated on the title page for each chapter). For this reason, there is some repetition of study site and species
descriptions between the chapters. Length and structure of these chapters follow the respective journal requirements, but general formatting including referencing (CDU_Harvard_2018), language conventions and other style details have been modified to a consistent style. A reference list follows each chapter.

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Chapter 2. Literature Review

2.1 Introduction

In the sections below, I first provide a general introduction to the bustards, focusing on the physical, behavioral, ecological and evolutionary factors that explain why they have such difficulty coping with rapid changes in the world around them. I also briefly review the threats to bustards at a global scale. I give greater attention to bustard species in tropical Asia because they are the most threatened and that is where this thesis is focused. I then introduce the study species – Bengal Florican *Houbaropsis bengalensis* – detailing the status, ecology, population, trends and the state of species-specific research and conservation, always with a greater attention to the population in Cambodia because that is the primary focus of the thesis. Lastly, I review conservation efforts directed towards other bustard species to elucidate details that can inform the research that constitutes the data chapters of this thesis and the conservation efforts that aim to prevent the extinction of Bengal Florican.

2.2 Bustards Otididae

2.2.1 Origins

Bustards evolved in the early Eocene (40-50 million years ago) and form a clade with cuckoos and turacos named Otidimorphae (Prum et al. 2015). A clade known as Columbaves groups Otidimorphae with Columbimorphae (pigeons, mesites sandgrouse and some other families) rather than with Gruiformes (cranes and other similar families) to which bustards were previously thought to be closely related. Data from mitochondrial and DNA and nuclear intron sequences indicate an origin in the
savanna of southern or eastern Africa, where most bustard species are still found (Pitra et al. 2002). While members of the order have spread through Europe, Asia and Australia, they are absent from the Americas.

2.2.2 Physical features and ecology

The 26 species of bustard are highly specialised to a terrestrial existence. They completely lack a hind toe, which means that they cannot perch and must spend their entire life on the ground (Collar 2019). Although volant, they are heavy and large-bodied, with relatively small, broad wings (Bevanger 1998). The larger bustard species are among the heaviest of all flying birds. Male Kori Bustard *Ardeotis kori* and Great Bustard *Otis tarda* have reached 18 and 19 kg respectively, and even the smallest bustard, the Lesser Florican *Sypheotides indicus*, weighs 450 g (Collar 2019). Bustards are omnivorous, feeding chiefly on plant matter, especially legumes, but also taking invertebrates and occasionally small vertebrates (Collar 2019). Food is obtained by walking slowly and pecking at food items on the ground with its stout dagger-like bill. Bustards are inimical to water, unlike other large-bodied, largely terrestrial birds such as cranes, storks and other waterbirds. This combination of physical and behavioral features renders bustards extremely vulnerable to predation. Bustards mitigate this risk through a combination of cryptic plumage to avoid detection by predators and hyper-awareness to detect predators in a timely manner. The eyes of a bustard are located such that it has almost comprehensive horizontal visual coverage, i.e. the blind-spot behind its head is tiny, which allows it to detect predators from any angle (Martin & Shaw 2010). Conversely, this means that bustards have highly constrained vertical visual coverage, so in flight bustards cannot see what
is in front of them if they tilt their head even slightly to look at the ground. Bustards spend much of their time in a highly alert state, and typically either flush at great distance or walk quickly into cover and crouch to avoid detection (Collar 2019). In gregarious species, such as Great Bustard, there is evidence that single birds show higher levels of vigilance than individuals in flocks (Wang et al. 2015). The upperparts of all bustard species are brown and intricately patterned so that they are difficult to detect from above by aerial predators. If present, areas of black, grey, white or rufous plumage are confined to the head, neck and underparts, usually only in the male.

2.2.3 Breeding

The majority of bustards are believed to be polygynous. All species show some degree of sexual dimorphism in plumage and size, which is related to mating systems, intensity of sexual selection and agility of display (Raihani et al. 2006). Bustards display and breed in exploded leks (Morales et al. 2001). Exploded leks differ from classical leks in that the displaying males are widely separated, and humans only perceive them as aggregated when they are viewed at an appropriate spatial scale. The mating systems of bustards require expansive, flat landscapes that are free of obstructions to allow males to be seen from a great distance (often >1 km), without which leks may cease to function. In most species of bustard, the male possesses impressive display plumes on the head and/or neck that are hidden from view under the body feathers when not in use. Most known bustard displays are complex and spectacular, although some are more reserved, for instance the male Little Bustard *Tetrax tetrax* simply calls from a mound with its neck feathers fluffed and sometimes
makes a small jump (Jiguet & Bretagnolle 2001). The incredible display of the Great Bustard has been extremely well studied. Females select males based on their age, weight and display effort (Alonso et al. 2010b), which are cued by the size of the whiskers and neck plumes (Alonso et al. 2010a), females also conduct a detailed inspection of the state of the cloaca of desirable males during the display (the cloaca is highly visible in displaying males) to judge fitness (Bravo et al. 2014). Location of the male within the lek is also an important fitness cue for females, so males engage in fighting and resource defense behavior to obtain the best spots (Alonso et al. 2012).

Terrestrial displays of most species involve inflating the gular pouch to expand the fluffy or filamentous neck-feathers, often accompanied by vocalisations, either while walking (e.g. Great Indian Bustard *Ardeotis nigriceps*) or running (e.g. the two Houbara species *Chlamydotis*). The smaller species such as some of the *Lophotis* and the floricans produce aerial displays. Displaying male Lesser Floricans each maintain display territories of 1.2–2.5 ha, within which they make a vertical fluttering leap 2 m into the air from a concealed location in long grass, dropping back down to the same spot; males leap approximately once per minute (depending on temperature and weather) to a total of up to 400 times per day (Ridley et al. 1985). In contrast, the display flight of the male Bengal Florican is given much less often (less than 10 times per day) and only in the early morning and late afternoon, it consists of a fluttering flight 4–10 m into the air followed by a glide forwards, then another brief flutter upwards to regain some of the height before finally gliding forwards to the ground (Sankaran 1996; Gray et al. 2009a). Bengal Floricans also have a terrestrial element to the display that is given before the aerial part, this is performed on a small raised mound in an area of very short vegetation, such that the male is visible from a long distance. Female floricans are larger than the males. Male bustards with largely
stationary or walking displays are larger than females, the Great Bustard exhibits the most extreme sexual dimorphism in mass of any extant bird species, with males up to 2.48x heavier than females at the peak of the breeding season (Alonso et al. 2009). Male bustards are smaller than females in species with largely aerial displays (Raihani et al. 2006). Lekking birds typically have female-biased populations, (Donald 2007). Data on adult sex ratios of bustards are only available for a few species, of which Great Bustard consistently shows female-biased populations (possibly due to hunting) (Donald 2007), and one sedentary population of African Houbara *Chalampydotis undulata* exhibits a ratio of 1.41 females to males (Alonso et al. 2020). Well-studied bustard species of various sizes, such as Little Bustard and Great Bustard, appear intermediate between ‘K’ and ‘r’ selected demographic strategies: although they are relatively long-lived, females are sexually mature at age 1 year (2 years for male Little Bustard), with the result that they can compensate for high juvenile mortality through a long life-time of reproductive output (Morales et al. 2002; Morales et al. 2005). Male bustards play no part in incubation or rearing of the chicks. Females typically nest within leks, where they utilize different micro-habitats to displaying males, favoring areas with longer or denser vegetation. The nest is a small scrape on the ground in which most bustard species lay one or two eggs that are incubated for 20–25 days. Fledging takes 4–5 weeks, and females stay with the young for up to one year (depending on the species), when those species that have been studied are particularly reliant on *Orthoptera* as a food source for the growing chicks (Collar 2019).
2.2.4 Distribution

Phylogenetic relationships within Otididae have not been investigated using modern DNA sequencing techniques, so limits of genera and species are still poorly resolved in some cases. The summary of species distributions below is based on the most recent research. There are 21 bustard species in Africa (81% of bustard species), where most savanna landscapes support up to three sympatric bustard species of different sizes (Collar 2019). Members of the same genus are usually allopatric. In Africa, two large, widespread species in the genus *Ardeotis* occupy savanna and Sahel habitats, whilst another four slightly smaller species in the genus *Neotis* inhabit different savanna areas across the continent. Of the medium and small bustards, the two species of *Lissotis* occupy savanna habitat, the three *Lophotis* are species of semi-arid landscapes, one of the *Eupodotis* is widespread in savannas whilst the other is restricted to high altitude grasslands in southern Africa, three of the *Heterotetrax* are found in semi-arid habitats of southern Africa whilst the Little Brown Bustard *Heterotax humilis* has a tiny range in the Horn of Africa and is probably more closely related to Little Bustard and not a *Heterotax*, the two *Afrotis* are restricted to southern Africa, although they superficially resemble floricans but are not closely related (Horreo et al. 2014; Collar 2019). In desert regions in Africa, Fuerteventura (Canary Islands: Spain), the Middle East and central Asia, bustards are represented by the genus *Chlamydotis*, with what was long-regarded as one species now treated as two allopatric, medium-sized species: African Houbara and Asian Houbara *C. macqueenii*, owing to genetic divergence and differences in the length, shape and position of display plumes, and differences in posture and vocalizations at various stages of the display (Gaucher et al. 1996). In Europe and temperate Asia (and marginally north Africa), bustards are represented by the sympatric Little Bustard and
Great Bustard, the latter probably representing two species (one highly threatened) owing to differences in facial plumes used in display, upper-part plumage, ecology and genetics (Kessler et al. 2018). Although the Palearctic bustards are geographically proximate to the tropical Asian bustards they are not their closest relatives (Pitra et al. 2002), bustards evidently colonized tropical Asia from Africa on at least two separate occasions.

Fossils of an extinct bustard species named *Vastanavis eocaena* dating from the Eocene have been found in India, because the species bears little resemblance to fossils found in Europe, it is thought to have traveled to Asia from Africa on the Indian plate that started drifting north-east during that epoch (Mayr et al. 2007). *Vastanavis* may be an extinct lineage, or it may be related to the two florican genera *Sytheotides* and *Houbaropsis*, which are each other’s closest relatives but are not closely related to any extant bustards (Horreo et al. 2014). There is a single species in each of the florican genera. Lesser Florican is a savanna species, now extremely sparsely distributed in peninsular India and south-east Pakistan. Bengal Florican is polytypic, with *H. b. bengalensis* in India and Nepal and *H. b. blandini* in Cambodia and Vietnam. It is the only bustard species in Southeast Asia. More recently, tropical Asia was colonized by the genus *Ardeotis*. Outside of Africa and the Arabian Peninsula this genus is represented by two closely related, morphologically similar species: Great Indian Bustard in South Asia and Australian Bustard *Ardeotis australis* in Australia and southern New Guinea (Indonesia and Papua New Guinea) (Collar et al. 2018). Although fossils have not been found, it is likely that the ancestor of Great Indian and Australian Bustards once inhabited the intervening savanna areas of what is now Indonesia, sharing the habitat with megafauna that were extirpated by
hominids in the late Quaternary period, such as a number of *Stegodon* species, a large vulture and a giant stork (Louys et al. 2007; Corlett 2010).

### 2.2.5 Threats

With the exception of the African animals on the continent where humans evolved, humans have decimated the megafaunal assemblages of the world (Barnosky et al. 2004). Megafauna is arbitrarily classified as species weighing at least 40 kg, but if that limit is revised downwards somewhat, then in Asia and Australasia, bustards can be regarded as some of the last vestiges of the world’s megafauna. The Great Indian and Great Bustards vie for the title of the heaviest bird in Asia, whilst the only birds that are heavier than bustards in Australasia and Africa are flightless Ratites. Eight (31%) bustards are considered globally Threatened, with an additional seven (27%) species classified as Near Threatened, which makes them one of the most threatened groups of birds worldwide (BirdLife International 2018a). The Australian Bustard and many of the African species are considered Least Concern because rates of decline have not recently been sufficiently severe to trigger IUCN Red List criteria, their distributions contain large areas of savanna or grassland that are relatively free from human influence. Threatened African bustards, such as Ludwig’s Bustard *Neotis ludwigii*, typically have small distributions in which infrastructure development has led to elevated levels of adult mortality (Shaw et al. 2016). All of the bustard species that inhabit Europe or Asia are globally Threatened or Near Threatened, and three of the four most at-risk species are found in tropical Asia (Collar et al. 2017).
In Europe and Asia, bustards face a wide range of threats. The low-lying, flat grassland and savanna areas that they inhabit have long been favored for agricultural development. In most countries, grasslands not already turned to agriculture are regarded as wasteland, and rarely inspire the levels of protection afforded to forests and wetlands (Parr et al. 2014). In India and Nepal, almost all remaining populations of Bengal Florican are now restricted to protected areas that were established long ago to protect populations of large charismatic mammals. In Europe and the parts of Southeast Asia where bustards remain, these mammals have long been extirpated or nearly so. In the absence of megafauna to maintain grassland and prevent succession, bustards are able to tolerate, and even thrive, in extensive traditional agricultural systems (Wolff et al. 2001; Wright et al. 2012). However, like many “farmland birds”, bustards cannot tolerate agricultural intensification (Palacín & Alonso 2018).

Intensive agriculture, as well as tree crops and root vegetables, are simply incompatible with bustard persistence. A reliance on arable pseudo-steppes in Europe and on traditional rice cultivation in South-east Asia brings bustards into close proximity to humans and their commensals, such as domestic dogs. Bustards are extremely sensitive to disturbance, flushing at great distance in response to humans, vehicles and aircraft (Sastre et al. 2009). Because their demographic strategy is intermediate between ‘K’ and ‘r’ selected, bustard populations decline rapidly if there are elevated levels of adult mortality. However, as large, fast flying birds, bustards are desirable hunting targets. Arab dignitaries take luxurious safaris across central Asia and northern Africa to kill many thousands of Houbara for sport with specially trained falcons, known as “technofalconry”, with up to 20,000 additional birds imported annually to Gulf States to be killed during the training of the falcons (Collar et al. 2017). In Russia, China, Spain and indeed almost all countries within its range, illegal
hunting of Great Bustard for food and/or sport constitutes perhaps the greatest threat to the species (Alonso et al. 2003; Kessler et al. 2013; Palacín et al. 2016; Collar et al. 2017). With their high wing-loading, low-aspect and reduced forward vision, bustards are more prone to collisions with power lines than any other group of birds (Martin & Shaw 2010). Economic development requires infrastructure networks to move goods and power. In densely populated areas such as Europe and South Asia this means that power transmission and distribution lines are ubiquitous, whilst power lines even extend through sparsely populated areas such as the Karoo in the South Africa and Uzbekistan in central Asia (Burnside et al. 2015; Shaw et al. 2018). A global review of bustard mortalities on power lines indicated that in areas where power lines cross areas with bustard populations there is a mean of 0.69 detected bustard collision fatalities per km per year, for more detail see Annex 1 of this thesis (Mahood et al. 2016). Collision rates of bustards on power lines are sufficiently high to cause declines and local extinctions (Shaw et al. 2018). Unfortunately line-marking methods of any description do not conclusively reduce mortality of bustards, although they do reduce impacts on other bird species (Jenkins et al. 2010). Mitigation of power line impacts on bustards can only be achieved through re-routing or burying power lines, which is typically costly, and technically and politically difficult (Bernardino et al. 2018).

2.2.6 Tropical Asian bustards

There is nowhere in the modern world so hostile to bustards as tropical Asia. Of the three tropical Asian bustards whose distributions are restricted to that area, the Lesser Florican is Endangered (although may be uplisted to Critically Endangered in the near
future if rates of declines can be quantified) and the Great Indian Bustard and Bengal Florican are Critically Endangered (BirdLife International 2018a). All three species were regarded as excellent game birds during the colonial era in South Asia, and their populations decimated as a result (BirdLife International 2018a). The Great Indian Bustard has undergone an especially catastrophic decline and is the rarest bustard (Dutta et al. 2010; Collar et al. 2015). In the nineteenth century it was considered ‘most abundant’ throughout open habitats in peninsular India and the eastern borderlands of Pakistan (Rahmani & Manakadan 1990; Ishtiaq et al. 2011), but it declined rapidly in the latter part of the twentieth century and probably numbered only 300–350 by the late 2000’s, although it was still widely distributed (Dutta et al. 2010). By 2014 it was almost completely restricted to Rajasthan in the north-west and by 2018 the population had declined to 140 ± 53 (Dutta et al. 2010; Collar et al. 2015; Collar et al. 2017). The contributing factors to the decline of Great Indian Bustard are many, but include agricultural intensification, a switch from annual to perennial crops, afforestation, grassland encroachment by agriculture, industrial and infrastructure development, collisions with power lines, illegal hunting, predation by domestic dogs, and mismanagement of protected areas that were established to protect it (Collar et al. 2015). The population of Great Indian Bustard is likely to be considerably smaller than official estimates suggest (N.J. Collar pers. comm.), and there is a very real danger that it will be the first continental Asian bird extinction of the twenty-first century. There is less published literature on the decline of Lesser Florican, and it is only very recently that there was any indication that it is rapidly declining (Collar et al. 2017). Population estimates have varied widely, ranging from 4,374 in 1982, 1,672 birds in 1989, 2,206 in 1994 and 3,530 birds in 1999 (Dutta et al. 2013). In 2017 a comprehensive survey was undertaken and the number of displaying males was
estimated at 340 (95% CI: 162–597), almost all of the birds were found on agricultural land outside of protected areas (Dutta et al. 2018). It is unclear how this number should be compared to earlier population estimates due to differences in survey methodologies. Bengal Florican is in a slightly better situation, in part because it is more widespread, but its existence is still extremely precarious. In the next section I summarize Bengal Florican distribution, population and trends, and then provide some details on the ecology and threats to the species, with a greater focus on the Cambodian population.

2.3 The Bengal Florican

Bengal Florican has two widely separated populations, corresponding to the two subspecies *H. bengalensis bengalensis* and *H. b. blandini*. These two taxa are extremely similar, but the differences between them have been understated in recent literature and because of their geographic distributions, they are rarely described in the same book. In the Handbook to the Birds of the World (HBW), the differences are stated as “race blandini apparently larger” (Collar et al. 2018). Based on eight specimens collected in Cambodia, the type description of *blandini* describes it as “closely resembling *H. b. bengalensis*, but differing in the rather richer colour of the plumage, in the black ornamental feathers of the male being shorter, the comparatively shorter wings and broader and flatter bill” (Delacour 1929). Nothing has been published since to indicate that the two taxa have been compared side-by-side and these differences found to be invalid, and the HBW quote is unreferenced. Anecdotal observations suggest that there may also be subtle differences in display behavior between the taxa, linked to the shape, length and position of the male’s
display feathers. Field observations indicate that breeding males in Cambodia have moderately-long, black neck feathers of a consistent length along the entire length of the neck, which they puff out when the neck is vertically extended (often termed “fat neck display”), holding this pose for minutes at a time prior to embarking on their display flight, which is a staggered arc (S.P. Mahood pers. obs). Males in India perform a similar display flight, but the terrestrial portion of the display aims to show off what (Dutta et al. 2013) describes as the “thick bunch of [black] feathers hanging under the breast” (which is absent from H. b. blandini), through “full fluffing of the neck resulting in the plumes being spread out fully like a fan” (Sankaran 1996).

2.3.1 Distribution, population and trends: summary

Although it has never been stated as such, it is apparent that Bengal Florican is the only bustard species that is entirely restricted to the floodplains of large rivers. H. b. bengalensis is restricted to grasslands in the floodplains of the Brahmaputra and Ganges rivers (India and Nepal). H. b. blandini is known from the delta of the Mekong River (Vietnam and Cambodia) and the floodplain of the Tonle Sap Lake (Cambodia) (Collar et al. 2018). There is no modern or historical evidence that Bengal Floricans occurred in the area between the distributions of the two taxa, which at least in historical times supported extensive areas of superficially suitable lowland floodplain habitat, and indeed still supports other grassland-restricted bird taxa that co-occur with Bengal Florican elsewhere. No genetic study has yet been undertaken to allow reconstruction of the biogeographic history of Bengal Florican and permit evaluation of taxonomic limits within the species. Nonetheless, it is a biogeographical impossibility that the two taxa were not at some point in time connected, and dating
their divergence might shed some light on the reasons why the species is now absent from floodplains in Thailand and Myanmar.

All Bengal Florican populations occur in landscapes that have been inhabited by people and farmed for thousands of years. In the last half century, however, humans have massively reduced the historical Bengal Florican population through hunting and almost range-wide habitat alteration, so modern data on populations and trends span a time period when global Bengal Florican abundance is probably at an all-time low.

All remaining populations of Bengal Florican are small and highly fragmented. The global population is officially stated as 350–1,500 individuals equating to 250–999 mature individuals (BirdLife International 2018a), although it may be considerably less (Collar et al. 2017). Based on trends in the Cambodian population the Bengal Florican was uplisted to Critically Endangered in 2007 (BirdLife International 2018a).

2.3.2 Distribution, population and trends: H. b. blandini

_H. b. blandini_ was described from specimens collected in January 1927 at Su Vu in what is now Svey Rieng Province, eastern Cambodia, in the Mekong Delta, close to the international border with Vietnam (Delacour 1929). In 1939 it was seen in north-west Cambodia in Battambang Province and reported from Kampot Province in the south-east (Eames 1996). There were no subsequent records until 1959 when a male was seen in Kompong Thom Province in the Tonle Sap floodplain in the center of Cambodia, and another bird was seen in 1960 in north-west Cambodia (Goes 2013). The next records were in March 1990 in what was to become Tram Chim Nature
Reserve, Tay Ninh Province, Vietnam, where birds were subsequently seen in small numbers until May 1999, and in Ha Tien Province where the remains of an adult male were found in 1997 (Eames 1996; Buckton & Safford 2004). These are the last records that can be traced from Vietnam.

In 1999, small populations of Bengal Florican were discovered in grassland close to Ang Trapeang Thmor (a reservoir on the north-western edge of the Tonle Sap Floodplain in Banteay Meanchey Province) and in the Tonle Sap Floodplain in Kampong Thom Province, Cambodia (Goes 2013). The Tonle Sap Floodplain was quickly identified as the global stronghold of the species, with potentially thousands of birds persisting in the late 1990’s and early 2000’s (Goes 2013), although these estimates were not validated at the time. The Cambodian population has been intensively monitored since 2005–2007 when surveys were conducted in all grassland patches thought large enough to support the species (Gray et al. 2009a). These were the first systematic surveys of the species. The population was estimated to be 416 (95% CI 333–502) displaying males (Gray et al. 2009a). Surveys were repeated using the same methodology in 2012, revealing that the numbers of displaying males had declined at approximately 11% per annum to 216 (95% CI 156–275) (Packman et al. 2013b). Since 1999 there has been only one record of Bengal Florican in the Mekong Delta: a female with chick in August 2015 at Bueng Prek Lapouv (in Cambodia but within sight of the international border with Vietnam) (J. C. Eames pers. comm.). The Mekong delta population can be inferred to be extinct or almost so.
*H. b. blandini* currently has the smallest distribution of any bustard taxon, but it is plausible that its distribution was much larger at certain points in geological time. Habitats in Southeast Asia have been shaped by cyclical ice-ages and interglacials over the past 2 million years. During glacial maxima, the sea level was much lower than today and southern Vietnam and Cambodia were connected by land to what is now Peninsular Malaysia by the now submerged Sunda Shelf, where it is thought that there were four large river basins (Sathiamurthy & Voris 2006). In Southeast Asia, floodplain habitats were therefore probably much more extensive during glacial maxima, and a band of savanna habitat spread across the Sunda Shelf to what is now Malaysia and Indonesia. This accounts for the faunal similarities between relictal savanna woodland in Java and Indochina (for example, the presence of Brown Prinia *Prinia polychroa* and Common Tailorbird *Orthotomus sutorius* in those locations but not, during the current interglacial, in the intervening part of Sundaland) (Bird et al. 2005). The flood regime of the Tonle Sap Lake has also been subject to massive change over time. Connected to the Mekong River by the Tonle Sap River, the Tonle Sap Lake is the world’s largest flood-pulse ecosystem. During October to June the Tonle Sap drains into the Mekong, but as the Mekong flow intensifies during May to September (the wet season) it forces water back up the Tonle Sap River into the lake. This causes the lake to expand in area from 2,400 km² to 7,000–13,000 km², with considerable inter-annual variation in flood extent (Kummu et al. 2014). The lake is relatively recent in origin, indeed during the most recent glaciation (approximately 20,000 years before present) the Mekong River entered the Sunda Shelf to the west of the lake, rather than to the east as it does now (Sathiamurthy & Voris 2006). As recently as 7,000–5,500 years before present the flood regime of what is now the
Tonle Sap Lake was much reduced and it functioned like a typical tributary of the Mekong (Penny 2006).

2.3.3 Distribution, population and trends: H. b. bengalensis

In South Asia, Bengal Florican are restricted to the alluvial floodplains of the Ganges and Brahmaputra rivers along the base of the Himalaya (Collar et al. 2018). These are geologically young rivers, and have shifted considerably, especially during glaciations, most recently in the late Pleistocene/early Holocene (Morgan & McIntire 1959; Heroy et al. 2003). The area of alluvial floodplain grassland, and the geographical location of that grassland, will have changed constantly over geological time. Historically Bengal Florican was much more widespread in the Gangetic and Brahmaputra Plains, and also occurred in Bangladesh where it is now extinct (BirdLife International 2018b). Less than 2% of alluvial grasslands remain intact in India (Dutta et al. 2013), although modelling indicates that the extent of suitable habitat for Bengal Florican in India is wider than usually assumed (Jha et al. 2018). Recent surveys continue to uncover previously unknown populations of significant size, such as those in unprotected grassland on the Brahmaputra River chaporis (islands) and the Daying Ering (D’Ering) Memorial Wildlife Sanctuary, Arunachal Pradesh (Rahmani et al. 2016a; Rahmani et al. 2016b). As a result of these surveys, Bengal Florican are known to breed in at least 15 sites in India, the exact number depends on how sites are defined, so far as is known Bengal Florican has been extirpated from most unprotected grasslands (Collar et al. 2017). Populations in some Indian protected areas have also declined, and although monitoring data are difficult to interpret, there have been local extinctions owing to hunting, encroachment,
inappropriate grassland management regimes, succession and hydrological processes (Collar et al. 2017). Population trends at important sites such as Manas National Park, Kaziranga National Park and D’Ering Wildlife Sanctuary are poorly known (Collar et al. 2017). The total population in India is estimated at 350–400 adult birds (Rahmani et al. 2016a) based on an estimate of 174–198 adult males and an assumption of a 1:1 sex ratio (Rahmani et al. 2016a; Collar et al. 2017; Rahmani et al. 2017).

In Nepal, Bengal Floricans have recently been found in only four areas, all protected: Shuklaphanta National Park, Bardia National Park, Chitwan National Park and Koshi Tappu Wildlife Reserve (Baral et al. 2003; Baral et al. 2012; Baral et al. 2013; Collar et al. 2017). The population in Nepal is estimated at approximately 100 birds (Collar et al. 2017). It is difficult to quantify population trends owing to spatio-temporal variation in survey methodology, but local declines have been noted (e.g. at Chitwan National Park) and the population in Bardia National Park may be extinct (Collar et al. 2017). More than half of the remaining birds are found at Koshi Tappu Wildlife Reserve (Collar et al. 2017). Reasons for the decline are similar to India, a mix of encroachment by local people and succession of grasslands to scrub caused by changing hydrological processes (due to damming upstream) and excessive burning to promote new grass growth for globally threatened herbivores or illegal cattle grazing (Baral et al. 2012).
2.3.4 Habitat preferences

As noted, the Bengal Florican is the only bustard species that is entirely restricted to floodplain grassland during the breeding season. There is no evidence that the breeding range of Bengal Florican has ever extended outside of floodplain areas into the savanna woodlands that dominated much of South Asia and monsoonal parts of Southeast Asia. In India and Nepal their restriction to floodplains could be assumed to be caused by inter-specific competition, but the savanna-dwelling Lesser Florican and Great Indian Bustard do not occur in Southeast Asia. Possibly the Bengal Florican’s reliance on floodplains of large rivers is a true habitat specialization, for unknown reasons, that may have always restricted its distribution.

The Bengal Florican breeds during the dry-season in grasslands and extensive traditional agricultural systems in the floodplains of large rivers. Originally it is likely that the floodplain habitats were maintained as suitable grassland habitat by large grazing animals. In Cambodia populations of Asian Elephant *Elephas maximus*, at least one of the two Rhinoceros species (both nationally extinct in or close to colonial times), four species of wild cattle and five species of deer (Corbet & Hill 1992) presumably migrated annually from the forested uplands that surround the Tonle Sap Lake to graze lush floodplain vegetation, as similar species still do in the hydrologically analogous Okavango Delta. A similar diversity of grazing herbivores has historically occurred in South Asian habitats and continues to do so in the protected areas where Bengal Floricans persist. In India and Nepal, Bengal Floricans breed in areas dominated by the grasses *Imperata cylindrica*, *Saccharum spontaneum*, *Erianthus munja*, *Vetiveria zizanioides*, *Narenga porphyrocoma*, *Cymbopogon*
*martini* and *Sclerostachya fusca* (in no particular order) (Jha et al. 2018). Grasslands used during the breeding season are flat, and have no more than widely scattered shrubs and bushes. Large herbivorous mammals continue to be abundant in these grasslands. Together with hydrological processes and (legal and illegal) cutting and burning, grazing by large mammals presumably helps to maintain habitat as grassland by preventing succession to scrub (Hobbs 1996).

In Southeast Asia *H. b. blandini* breeds in areas of relict grassland and agricultural land in the floodplain of the Tonle Sap Lake, Cambodia, and at least formerly throughout the Mekong delta of Cambodia and Vietnam (Collar et al. 2018). In Cambodia, breeding birds prefer areas of relatively short tussocky *Imperata* grass, recently burnt tracts, or long grass grazed down to c. 50 cm high, feeding in the shorter grass, and retreating in the hotter parts of day to areas with longer grass (Gray et al. 2009b). Males in particular prefer recently burned areas, presumably because their displays can be seen from a greater distance, whilst females need areas of longer grass in which they can safely nest (Gray et al. 2009b). Floricans in Cambodia also formerly bred in fallow fields that in the wet (flooded) season had been used to cultivate deep-water rice, which leaves a long, bunchy stubble after harvest (Gray et al. 2007).

During the non-breeding season, Bengal Florican breeding in India and Nepal use areas characterised by a relatively low human population density, near-absence of permanent infrastructure, and relatively low-intensity agricultural production of crops such as sugarcane, mustard, lentil, rice and wheat, intermixed with fallow plots and
intensively grazed grasslands dominated by *Typha angustifolia, Saccharum spontaneum, Phragmites karka, Cynodon dactylon* and *Imperata cylindrica* (Jha et al. 2018). Hydrological processes preclude agricultural intensification in these areas, so trends in habitat, if not trends in disturbance, are likely to be stable (Jha et al. 2018). During the non-breeding season in Cambodia, Bengal Floricans preferentially select areas under grassland cover or fallow wet-season rice fields, as well as open, grassy savannah (or medium-canopy) woodland (even young rubber plantations), in contrast, they avoid areas of bare ground, cassava, closed canopy woodland and mature tree plantations (Hillard 2012).

2.3.5 *Breeding ecology*

Like most bustards, Bengal Florican has an exploded lek breeding system, >4 males are required for a lek to function (Gray et al. 2007) and each male needs up to 2.5 km$^2$ of habitat from which to display (Gray et al. 2009b; Packman 2011). Breeding occurs in the dry season: February–August in Cambodia, March–June in India and Nepal), and there is some evidence that females can lay a second clutch if the first fails (Packman 2011). As is typical for a bustard, clutches range from 1–2 eggs laid in a scrape in thick grass cover, and eggs are incubated for c. 25–28 days (Collar et al. 2018). Chicks have rufous-buff down marked with rufescent brown and are cared for by the female alone (Collar et al. 2018). Age of female at first nesting is not known. Bengal Floricans are omnivorous, like other known bustard species *Orthoptera* are an important food source, especially during chick-rearing (Dutta et al. 2013). Local people who use the Tonle Sap grasslands report to Cambodian Bengal Florican
conservationists that Bengal Floricans also feed on a wide variety of shoots, leaves and small flowers or berries, favouring leguminous species (Son Virak pers. comm).

2.3.6 Migration

Bengal Florican must migrate annually from their floodplain breeding habitat to escape rising floodwaters. This appears to be a flexible behavior, because in years when the maximum flood extent of the Tonle Sap Lake does not inundate the breeding grounds, at least some Bengal Floricans do not migrate (Packman 2011). However, in India, birds breeding in areas that are not inundated exhibit similar migratory behaviour to those breeding in areas that are inundated (Jha et al. 2018). Abundance of favoured food or ability to capture food, linked possibly to annual changes in habitat structure induced by the monsoon, may also be an important motivation for birds to migrate. Typically, the first stage of migration appears to involve a relatively short distance movement (<10 km) to what are conceivably staging grounds, followed by a longer distance movement (but <80 km, based on a sample of 32 satellite tagged birds (4 in India, 7 in Nepal, 21 in Cambodia)) to non-breeding grounds (Packman 2011; Jha et al. 2018). Birds wander moderately widely within non-breeding areas, and return to their relatively small breeding territories soon after the end of the wet season (Packman 2011; Jha et al. 2018). Little Bustards are nocturnal migrants and make many short stops when on migration (Alonso et al. 2019), anecdotal data indicate that Bengal Florican do the same. Multi-year telemetry indicates that individuals have discrete breeding and non-breeding territories to which they return annually (Packman 2011; Jha et al. 2018).
2.3.7 Management: summary

Bengal Florican receives the highest level of legal protection available in all of the countries where it occurs, but grasslands do not attract the same conservation interest as forests and wetlands, and a grassland bird is less likely to capture the public or political imagination than a rhinoceros or elephant. Nonetheless, these birds are spectacular megafaunal relicts, especially in Cambodia where they are one of the largest-bodied species remaining in the grasslands of the Tonle Sap Floodplain. Despite the distinctive and charismatic display of the breeding male, the Bengal Florican has little known local cultural significance anywhere in its range, unlike some other bustard species e.g. Asian Houbara. Nevertheless, as a showy bird species in a highly threatened group, the species does have significance to conservationists globally and they aim to use every tool available to try and prevent the extinction of the species. Here I summarize the research and management situation for Bengal Florican. I go into greater detail for *H. b. blandini* because it is the subject of this thesis.

2.3.8 Management: *H. b. bengalensis*

In India and Nepal research has focused on understanding the vegetation characteristics of breeding habitat (species composition, height, and structure), as well as the impacts of threats such as hunting, overgrazing, over-exploitation of grasses for thatch, and the adverse impacts of grassland management for large wild herbivores (Dutta et al. 2013; Rahmani et al. 2016a). As yet, there has been little opportunity to apply this research and influence grassland management for Bengal Floricans in India.
and Nepal, because protected area management practices are optimized for large threatened herbivores such as Indian Rhinoceros *Rhinoceros unicornis* (Dutta et al. 2013). However, the fact that almost all Bengal Floricans breed in protected areas itself confers a degree of protection to their populations, without which they might be very much scarcer. The presence of humans in grasslands has traditionally been regarded as a threat to Bengal Florican, because people take or accidentally trample their eggs and generally cause disturbance, but it is increasingly recognized that an intermediate level of traditional community use of grasslands is advantageous for Bengal Florican because the actions of people and cattle prevent scrub encroachment (Dutta et al. 2013). Although this has not been stated, it is also possible that the presence of local people in a grassland area dissuades protected area management authorities from managing the grassland for large wild herbivores such as Indian Rhinoceros. Research into non-breeding season habitat preferences and movements has only recently begun, but results to date indicate that Indian Bengal Floricans behave similarly to those in Cambodia (Jha et al. 2018). Nonetheless there is an urgent need to use these data to address threats in the non-breeding grounds, which based on current knowledge are almost entirely outside of protected areas.

2.3.9 Management: *H. b. blandini*

In Cambodia, research conducted soon after birds were rediscovered in 1999 indicated that the Bengal Florican was subject to extremely heavy market-driven hunting (Davidson 2004). The numbers of Bengal Florican that were recorded at markets in 1999 are difficult to comprehend in a modern context, with estimates of 300–600 birds sold annually on roadside food stalls in Kompong Thom town (Goes 2013).
Hunting was rapidly brought under control through legal protection of Bengal Florican in 2002, which completely banned hunting, and an advocacy campaign conducted by Wildlife Conservation Society (WCS) and the Forestry Administration (part of the Ministry of Agriculture, Forestry and Fisheries: MAFF) (Goes 2013).

Evidently the rich ethno-cultural landscape of the Tonle Sap Floodplain had long been a highly suitable breeding habitat for Bengal Florican (Gray et al. 2007). In the absence of wild ungulates, grasslands in the Tonle Sap Floodplain were an important grazing ground for vast herds of domestic cattle that, together with burning to promote grass-growth, prevented succession to scrub (Packman et al. 2013a). Cambodia was at one time home to nearly one third of known rice varieties, many of them were specially adapted for the particular farming conditions of the Tonle Sap Floodplain but, along with much else, the majority of these, including the 15 most widely used deep-water varieties, were lost during the Khmer Rouge years (Home 1997). Traditional deep-water rice created a mosaic of habitats after it was harvested at the beginning of the dry-season: the stubble of deep-water rice can be more than 1 m in length, so clumps provided suitable habitat for nesting female floricans, whilst areas of burned stubble were used by displaying males (Gray et al. 2009b).

As traditional agriculture waned in the 2000s, research evaluated the adverse impacts of agricultural intensification on breeding floricans (Packman et al. 2013a; Packman et al. 2013b). Deep-water rice varieties were almost completely replaced by irrigated dry-season rice during the late 1990’s and early 2000’s, when wealthy elites took possession of the land and rapidly converted much of the best grassland. Irrigated dry-
season rice is a far less suitable agro-ecological habitat for breeding Bengal Floricans: birds can tolerate it if only one crop of dry-season rice is grown each year, the females can nest in desiccated head-ponds used for irrigation of rice where a lack of access for cattle allows grass to grow to a greater height (Gray et al. 2009b). However, if more than one crop of irrigated dry-season rice is grown per season and the land is underwater through to June (rather than March) then there is insufficient time for Bengal Floricans to breed successfully before the flood-waters of lake rise (Ibbett et al. 2019).

Agricultural intensification also had a unexpected consequence: the construction of irrigation canals blocked the traditional migration routes of cattle herders, and consequently led to a decline in grassland cover of 23% between 1995 and 2005 owing to scrub encroachment in the inner floodplain grasslands (Packman et al. 2013a). The Bengal Florican decline in Cambodia between 2005–2007 and 2012 is thought to have been a direct consequence of agricultural intensification (Packman et al. 2013b).

The first protected areas for Bengal Florican, known as Integrated Farming and Biodiversity Areas (IFBAs) were established under provincial decree in 2006. The IFBAs protected 35,400 ha of floodplain breeding habitat (Gray 2008). In 2010 their protection status was upgraded by ministerial decree (under the Ministry of Agriculture Forestry and Fisheries: MAFF) and their name changed to Bengal Florican Conservation Areas (BFCAs). This conferred a greater level of protection to the sites, but the number of sites and the area under protection in the breeding grounds were reduced to four and 17,331 ha respectively, after pressure from commercial rice cultivation interests (Packman et al. 2013b). At the same time, two BFCAs were established in putative non-breeding areas, totalling 13,828 ha. Satellite telemetry has
since elucidated the behavior of Bengal Floricans in the non-breeding season, revealing where they go and what their habitat preferences are (Packman 2011; Hillard 2012). Unfortunately, the opportunity to establish protected areas in the non-breeding range came before research into post-breeding dispersal had been completed, so sites had to be selected based on the best available data at the time. One of the two selected sites, Trea Sameakii BFCA, contains the most important non-breeding habitat for the best protected breeding population of Bengal Florican, whilst the other site, Tuel Kruel Pham Neum BFCA, supports the correct habitat but is slightly too far from the breeding grounds: there has only ever been one Bengal Florican record (WCS unpublished data). The addition of protected areas in the non-breeding grounds brought the total area under protection to 31,159 ha. In 2016, the management of the BFCAs was transferred to Ministry of Environment (MoE) and the protected status was upgraded to prime-ministerial sub-decree, the highest level of legal protection. The name of the protected area was changed to Northern Tonle Sap Protected Landscape (NTSPL), but individual parcels of protected land are still referred to as BFCAs for ease of reference (Figure 1). From the time of the IFBAs to the NTSPL, the regulations of protected areas established to protect Bengal Floricans have promoted sustainable community use of grassland (e.g. for grazing), with financial and technical support provided by WCS.
2.4 Future management needs: lessons from elsewhere

Bustards in Europe have benefitted from decades of in-depth research and conservation. To prevent the extinction of Bengal Florican in Cambodia, and indeed to prevent the extinction of bustards in tropical Asia, there is a need to apply best practice from other parts of the world where solutions have already been tested on similar species that face similar threats. In this section I discuss threats that are common to bustards in Cambodia and other parts of the world, document the drivers of those threats and evaluate the effectiveness of the solutions that have been tested to date.
2.4.1 Agricultural intensification

Whilst agricultural intensification is a relatively new phenomenon in Cambodia, and is yet to reach some parts of the Brahmaputra floodplain in India, agricultural changes since the 1970’s have already caused catastrophic declines in birds of open country and grassland (hereafter farmland birds) in Europe (Donald et al. 2001; Donald et al. 2006). The Common Farmland Bird Index, which tracks population trends in 39 species of farmland birds across Europe, indicates that populations declined by nearly 60% between 1980 and 2015 (Gregory et al. 2019). Declines in some species have been even more acute, and it has been possible to establish causal relationships between changes in specific agricultural practices and demographic trends in some farmland bird species (Donald et al. 2002). In western Europe, bustards have been particularly heavily affected by agricultural intensification. In France, the Little Bustard population that breeds in agricultural areas declined by 96% in 35 years, dropping from an estimated 7,500 breeding males in 1979 to 330 in 2016 (Bretagnolle et al. 2018b). Rates of decline of this magnitude are typically only seen in naïve island endemics that are exposed to novel predators, but they are comparable to those experienced by Bengal Florican in Cambodia since the mid 2000’s (Packman et al. 2013b).

The term ‘agricultural intensification’ covers a suite of measures that are designed to increase crop yields by maximizing the proportion of primary production available for human consumption (Matson et al. 1997). These measures include landscape-level interventions such as increasing field sizes or specializing in a smaller number of
crops, as well as changes to farming practices at the farm-level, such as mechanization, increasing chemical inputs, shortening crop rotation cycles or switching to higher yielding varieties (Tscharntke et al. 2005). In Europe, agricultural intensification is enshrined in the Common Agricultural Policy (CAP), which is the farming policy for all of the countries in the European Union (European Commission 2018). Launched in 1962, the CAP aims to support farmers and ensure a stable supply of food by promoting intensive farming through a system of subsidies that in 2016 accounted for 41% of the total EU budget (European Commission 2016). The CAP protects farmers with regulations to ensure that higher yields are guaranteed to result in higher incomes, which forms a strong incentive for intensification. The CAP guarantees fixed prices for goods (below which the EU is the buyer), which it protects by imposing taxes on cheaper imports, and it also enables farmers to invest by providing capital grants for mechanization and modernization (Donald et al. 2002).

Agricultural intensification has predominated in northern and western Europe for longer than in southern Europe where traditional farming systems are mixed, with small field sizes and an abundance of non-farm habitats (Stoate et al. 2001). Low densities of livestock are grazed on multi-year fallows, which maintain characteristic communities of plants, invertebrates and birds (Moreira & Leitão 1996). Extensive agricultural systems are ideal habitats for bustards, indeed Little Bustard only colonized the natural steppe habitats of southern France in the 1950’s when the spread of extensive agriculture had caused the conversion of 40% of the steppe (Wolff et al. 2001). The introduction of the CAP to the extensive, low intensity farming systems of southern Europe led to a range of adverse impacts on these habitats. In some areas, stocking densities were increased in arable steppes because livestock payments were
per head, leading to degradation of fallows, a reduction in the abundance of invertebrates, and declines in farmland birds (Stoate et al. 2001). Cropping systems were simplified as farmers sought to maximize revenue, leading to declines of birds such as Little Bustard in which males and females require different habitats during the breeding season (Salamolard & Moreau 1999). To eliminate the need for fallows, farmers took advantage of grants to install irrigation systems, which meant that irrigation pivots and power lines were introduced to areas where they were previously lacking (Stoate et al. 2001). Conversely, the CAP also drove farmers to abandon areas of marginal farmland and farms that were too small to qualify for payments, in some parts of Europe this is a greater concern for farmland birds such as bustards than agricultural intensification because of scrub encroachment (Queiroz et al. 2014).

Modernization and mechanization of farming has also reduced the suitability of farmland for wildlife. Modern crop varieties grow faster and are higher yielding than traditional varieties, which means that multiple crops can be grown on land where previously only a single crop was grown, but production is highly reliant on the use of chemicals. Fertilizers and herbicides ensure that crops grow at the expense of the non-crop plant species on which invertebrates and birds typically depend. High-yield crops are particularly attractive to pests, and therefore require higher rates of pesticide application. Pesticide use increased significantly in Europe and North America during the twentieth century, and although some of the most damaging pesticides have been prohibited and there have been various government initiatives to reduce their use, the negative effects on non-pest plant and animal species persists (Geiger et al. 2010).
The CAP underwent reform in 1992, in part because subsidies were producing a vast surplus of crops that was costly for the EU to store and difficult to sell. New policy instruments were developed which could reduce this problem and achieve environmental objectives. The first was the Birds and Habitats Directive (79/409/EEC,92/43/EEC) that mandated member states to develop agri-environment schemes to attempt to alleviate some of the adverse consequences of agricultural intensification, with funding provided where these had costs to farmers (Stoate et al. 2001). These built on the Agricultural Structures Regulation of 1985, which was essentially an environmental compensation scheme, and were taken further under the 1998 Agenda 2000 reform, which created additional opportunities for different countries to develop agri-environment schemes in different ways (termed environmental cross-compliance) (Hodge et al. 2015). Under Agenda 2000, farmers were able to obtain support for activities other than farming, which meant that in some locations governments could use this funding for conservation of important farmland habitats, with payments contingent on compliance with environmental restrictions (Henle et al. 2008). Farmer participation in agri-environment schemes is entirely voluntary. The EU also promoted more sensitive farm management through the EC Directive on the Conservation of Wild Birds (79/409/EEC), which established a network of Special Protection Areas (SPAs), and the EC Habitats Directive (92/43/EEC), which identified Special Areas of Conservation (SACs). Taken together these are known as Natura 2000, which forms the largest coordinated network of protected areas in the world, covering 18% of the EU’s land area. An alternative approach to farming is promoted by the EU through more than 800 active LIFE-Nature projects, in which land is purchased to be managed for biodiversity purposes or farmers incentivised to manage it for biodiversity (Henle et al. 2008).
Agri-environment schemes were initially developed to protect threatened habitats, but over time their role shifted towards preventing the loss of farmland wildlife, particularly birds, more recently they came to be regarded as tools to maintain ecological services that are beneficial to farming, such as populations of pollinators (Ekroos et al. 2014). Their success has been the subject of a large number of case studies and at least three meta-analyses, a meta-analysis of these indicates that agri-environment schemes can be effective for conserving wildlife on farmland, but they are expensive and need to be carefully designed and managed (Batáry et al. 2015). Agri-environment schemes have been broadly unsuccessful at preventing the decline of threatened Mediterranean farmland birds (Palacín & Alonso 2018). The most successful agri-environment schemes have tended to be those that have focused on specific species and/or take areas of farmland out of production, and are supervised by scientists. In contrast, non-targeted schemes that aim to support an environmentally sensitive approach to farming (e.g. organic) usually only benefit common species and have little overall impact (Batáry et al. 2015).

2.4.2 Management of agricultural areas for bustards

Agri-environment schemes have played a key role in conservation of bustards in Europe over the past two decades. Drawing from literature on Little Bustard, I summarize why and how these agri-environment schemes were developed, and the successes and failures of this approach to bustard conservation.
In France, agri-environment schemes are mainly five-year contracts between volunteer farmers and the government (Berthet et al. 2012). The best studied is the “Zone Atelier Plaine & Val de Sèvre”, a complex of eight SPAs in Poitou-Charentes covering >160,000 hectares, which has been the subject of a network of Long-Term Socio-Ecological Research (LTSER) studies managed by the Centre for Biological Research of Chinzé (CEBC–CNRS) (Bretagnolle et al. 2018a). In this area there had been a reduction in mixed farming systems in favor of intensive cereal crops that were incentivized under the CAP, leading to a decline in cattle and goats and with them the meadows and semi-perennial forage crops on which they grazed. This led to a rapid decline in the Little Bustard population (>10% per year), demographic modelling indicated that in the early 2000’s there was a 45% chance of extinction of the migratory French population within 30 years owing to high adult mortality and low fecundity (Inchausti & Bretagnolle 2005). Models indicated that the probability of extinction was particularly sensitive to declines in the proportion of females, which are vulnerable to mortality during mechanical harvesting operations when they are nesting (Morales et al. 2005). Extinction risk was doubled owing to Allee effects specific to lekking species: male Little Bustards abandon an area if local lek size drops below six individuals (both sexes) (Morales et al. 2005).

By the early 2000’s this Little Bustard population required immediate conservation intervention to prevent its extinction (Berthet et al. 2012). One management option might have been to establish a strictly protected nature reserve from which farming was excluded, but this idea was quickly abandoned during the planning phase because prohibitively large areas of land would have been needed and the region was already under intensive cereal production (Berthet et al. 2012). The use of land sparing
approaches for the conservation of open-habitat bird species has been criticized, and land sharing approaches are frequently regarded as the best compromise (Wright et al. 2012), but see below. Between 1996 and 2001, a LIFE-Nature program had trialed experimental attempts to reduce the rate of decline by increasing insect abundance and protecting nests during harvesting, but this failed because not enough farmers joined the scheme (Inchausti & Bretagnolle 2005). Nonetheless it generated useful biological data and provided an indication of the kind of alternative farmland management measures that might benefit Little Bustard under a land-sharing framework (Bretagnolle et al. 2011). This led to development of eight agri-environment schemes at a landscape scale in Poitou-Charentes and reinforcement of the wild population by captive-reared birds (Jolivet & Bretagnolle 2002; Bretagnolle & Inchausti 2005). Here I first discuss the agri-environment schemes, captive management of bustards is discussed later.

The agri-environment schemes that began in Poitou-Charentes in 2004 sought to re-integrate grasslands within the agroecosystem to improve productivity and reduce mortality of females (Berthet et al. 2012). In agricultural areas, male and female Little Bustards have requirements for areas with different vegetation structure during the breeding season (Morales et al. 2008). Research showed that crop height was more important than crop type for displaying males (Martínez 1994), birds select fields of alfalfa, set-aside, flax and sunflower, which are all short in height during the display season, and actively avoid cereals, maize and oilseed rape (Salamolard & Moreau 1999). Females nest between May and August, they favor fields of set-aside and alfalfa, which have longer vegetation during the nesting season and a higher density of insects (Salamolard & Moreau 1999; Morales et al. 2013). In areas where suitable
insects are at low density, females wander widely to obtain food and chick mortality is extremely high, so it is critical to maximize abundance of their favored insects in breeding areas (Lapiedra et al. 2011). Little Bustards in the French SPAs migrate to Spain in the non-breeding season (Villers et al. 2010). Winter habitat preferences of Little Bustard show similarities to breeding habitat preferences, for instance, in Portugal, they prefer recent fallows with vegetation that is relatively short (11–20 cm) and sparse (11–50% cover), and they avoid areas used frequently by people (Silva et al. 2004).

Under the agri-environment schemes promoted in the SPA, farmers were compensated for delaying the mowing date of alfalfa fields, maintaining fallow areas and field border habitats, and reducing pesticide inputs (Morales et al. 2005). In order to make these alternative management measures attractive to farmers, they were designed so that their restrictive nature was as limited as possible (Berthet et al. 2012). Alfalfa fields were traditionally mowed between May and July but under the agri-environment schemes farmers were contracted to delay mowing until after 31 July to prevent destruction of nests, eggs, broods and nesting females, this meant that farmers lost two harvests each year, for which they were financially compensated (Bretagnolle et al. 2011). To increase the abundance of insects, a landscape-scale experimental approach was adopted, which set a target of 15% of the agricultural land under a management regime that made it suitable for insects (Berthet et al. 2012). Farmers were compensated for converting annual cereal crops into grassland meadows and fodder crops and/or not using pesticides and herbicides in grasslands (Bretagnolle et al. 2011). By the late 2000’s more than 1,200 hectares of farmland in
Poitou-Charentes were under the agri-environment schemes (Bretagnolle et al. 2018b).

There was a five-fold increase in the number of male Little Bustards in Poitou-Charentes following the implementation of the agri-environment schemes between 2004 and 2009 (Bretagnolle et al. 2011). Alfalfa fields were used preferentially by breeding females, less than 10% of nests in fields under agri-environment schemes were destroyed by mowing operations (Bretagnolle et al. 2011). The abundance of grasshoppers was higher in the agri-environment scheme fields, and productivity and populations of Little Bustards increased accordingly (Bretagnolle et al. 2011). However, the short-term success of the agri-environment schemes was undermined by an increase in market prices for cereals and the 2014 CAP reforms, which changed the financial incentives offered to farmers and resulted in the termination of all of the farmer contracts in 2015 (Bretagnolle et al. 2018b). Little Bustards continued to nest in alfalfa fields where they were available, but because post-2014 the mowing regulations were no-longer in place, these nests were destroyed and these meadows now acted like an ecological trap (Bretagnolle et al. 2018b). Published data are not available to evaluate impacts at a population level, however it is highly likely that these changes have caused the population to decline. Thus, although initially highly successful, agri-environment schemes ultimately failed to conserve Little Bustard within an intensive agroecosystem because they relied on market forces and payments that could not be maintained over time. Neither of these variables were under the control of conservationists. The conclusion of the trial was that low impact agriculture is currently critical to bustards in Europe and Asia, but if agricultural intensification cannot be legally prohibited at scale, then a land-sparing approach that involves
establishing protected areas might be more appropriate for bustard conservation (Bretagnolle et al. 2018b; Palacin & Alonso 2018).

2.4.3 Management of protected areas for bustards

In Europe, protected areas typically include farmland so they cannot be considered a land-sparing approach. In the SPAs discussed above, and in Portugal and Spain these ‘protected areas’ have failed to halt the decline of Little Bustards despite the use of agri-environment schemes (Bretagnolle et al. 2018b; Casas et al. 2018; Silva et al. 2018). In grassland landscapes that support only species with small area requirements, such as in South America, strict protection of a relatively small proportion of grassland is predicted to be better for threatened birds than preventing agricultural intensification over a wider area (Dotta et al. 2016). However, protected areas for bustards must be large owing to their home range requirements. In Africa, large, strictly protected areas that were established prior to conversion of savanna to agriculture and pasture are likely to be part of the reason for the lower threat status of bustards, even if these protected areas are not managed for the purpose of bustard conservation. Areas with bustard populations that are already under some form of agriculture could theoretically be returned to grassland or low intensity agriculture under the strict regulatory framework of a traditional top-down protected area management regime, but the extremely high cost of agricultural land generally precludes this approach in most areas.
Even when grassland protected areas have been established, they are notoriously difficult to protect. In North America where regulatory frameworks are relatively strong, conservation easements have been shown to prevent conversion of grassland to cropland (Braza 2017). In contrast, grassland protected areas in India and Nepal that were established for large charismatic mammals, but are now critical for bustards, are frequently subject to encroachment by agriculturalists or cattle herders (Dutta et al. 2013). Some protected areas that were established specifically to protect bustards have fared even worse. In India, large areas of grassland in protected areas established to protect Great Indian Bustard were regarded as “wasteland” under Forest Department policies, and government financing was provided to plant tree species (even exotics) to turn them into “forests” (Dutta et al. 2010). Other Great Indian Bustard Reserves were far too small for their purpose and subject to well-intentioned mismanagement or encroachment (Dutta et al. 2010). Stoung-Chikreang BFCA in Cambodia has also received criticism for its small size, whilst Chong Duong BFCA has been almost completely encroached and has lost its Bengal Florican population (Packman et al. 2013b).

Protected areas can help to reduce illegal hunting of bustards, which was the primary cause of the decline in Spain’s Great Bustard population (Casas et al. 2018). That population is now increasing, as a result of stricter enforcement of the hunting ban, both inside and outside of protected areas, combined with an agri-environment scheme which promoted unirrigated legumes (Martin et al. 2012), although there is disagreement over whether reduction of hunting alone might account for the population increase (Casas et al. 2018). No-hunting reserves are particularly important for disturbance sensitive birds, even if they are not being hunted, for instance, in
France Little Bustards preferentially use no-hunting reserves on days when legal hunting of other species is permitted (Casas et al. 2009).

Where it is possible to establish, strictly protect and sensitively manage protected areas they are likely to be the most successful approach for bustard conservation. However, to date it has proved impossible to do this at the scale that is necessary for bustard conservation. In this context it might be argued that other approaches to land management, such as conservation concessions or private reserves may be more suitable (Gray et al. 2019). However, these are not a panacea. They are likely to face similar issues to government-managed protected areas, such as a lack of suitable, available habitat to protect in the first place, and the challenge of preventing encroachment without an ethically contentious military-style approach to boundary defense.

2.4.4 Captive management for bustards

Captive management allows conservationists to reduce the influence of damaging externalities associated with management of bustards in agro-ecological systems and protected areas. Humans have been keeping bustards in captivity for over 100 years, although not always for the purpose of captive-breeding, nearly half of the world’s bustard species are under some form of captive management (Collar 2019). Captive management of bustards takes several different forms, including head-starting, translocations, and large-scale population supplementation using captive-bred birds. Captive management can also have many different objectives, here I focus on the
impact of captive management strategies on the conservation of wild bustard populations.

2.4.5 Head-starting

A captive management program that aimed to release 100 head-started Little Bustards over five years was implemented in parallel with the French agri-environment schemes discussed above (Bretagnolle & Inchausti 2005). Between 2003 and 2007 the scheme reared and released approximately 350 fledglings (2 months old) that were sourced from nests that would have been destroyed by farming activities (Villers et al. 2010). Head-starting Little Bustards in captivity did not alter the migratory behavior of this population, which winters in Spain, and the hand-reared birds migrated and behaved normally on their return to the breeding grounds in France (Villers et al. 2010). It is likely that head-starting contributed to the temporary increase in this Little Bustard population, but this cannot be quantified (Bretagnolle et al. 2011). However, as migratory behavior in bustards is at least partially heritable, birds for re-stocking should be locally sourced where possible (Villers et al. 2010). In 2003 six fledglings that had been sourced from eggs collected in central Spain were released into the French population (Villers et al. 2010). Little Bustard populations in Spain and Portugal exhibit a variety of short-range migratory strategies that differ from those of the French-breeding population, whilst some are completely sedentary (García De La Morena et al. 2015). Satellite telemetry indicated that the Spanish birds that were released in France did not migrate (Villers et al. 2010).
2.4.6 Translocations

In several European countries, including Germany, Romania and the United Kingdom (UK), programs have been established to reintroduce or re-stock Great Bustard populations in locations where they are extinct or almost so (Osborne 2005; Garlea et al. 2013). It has generally proved impossible to produce enough bustard chicks in captivity to make these reintroduction attempts possible, so translocation of captive-reared birds from wild donor populations has been considered the only viable option (Osborne 2005). Progress and impact of the reintroduction in the UK, where it had been extinct since the 1800’s, is particularly well documented so I use it as a case study here.

Up to 2014, 484 Great Bustard chicks were rescued from wild nests in Russia and Spain that would otherwise have been destroyed by agricultural operations, and of these, 200 birds have been released on Salisbury Plain between 2004 and 2014 (Burnside et al. 2012; Ashbrook et al. 2016). Post-release survival of Great Bustards in the UK was initially low as a result of predation by Red Fox *Vulpes vulpes* and collisions with powerlines and agricultural fences, captive-reared Great Bustards released in Germany experienced similar levels of mortality due to predation by Red Fox and White-tailed Eagle *Haliaeetus albicilla* (Burnside et al. 2012). Such high post-release mortality is likely a result of naivety: captive-reared birds often lack essential skills such as predator recognition that are learned from parents and conspecifics (Griffin et al. 2000). Wild-born Great Bustards spend at least the first six months of life with the female parent (Martín et al. 2008). Bustards are generally extremely vulnerable to collisions with power lines, but it is possible that there was
elevated mortality among reintroduced Great Bustards due to poor musculature, feather condition and flight performance, which are problems frequently shown by captive-reared birds of other taxonomic groups e.g. (Hess et al. 2005).

Release methods for Great Bustards were modified in 2009 to allow birds more time to practice foraging and flying in a safe environment prior to release, and modified again in 2012 to incorporate dehumanization of released birds to reduce tameness (Ashbrook et al. 2016). This did not have the desired impact on mortality rates, and as of December 2014 the reintroduced Great Bustard population comprised five females and four males greater than one year of age (Ashbrook et al. 2016). In 2014 a decision was taken to only source birds from Spain, which meant that rearing and release methods could be further modified because they were no longer subject to the quarantine restrictions imposed by bringing birds from outside the EU, a process that may have contributed to the low fitness of released birds (Manvell & Goriup 2017). Although the UK Great Bustards established a lek and began breeding in 2007, with the first successful nesting in 2009 (Burnside et al. 2012), chick survival was extremely low up to 2014 and there was no recruitment to the population (Ashbrook et al. 2016). However, chicks hatched in 2016 had a >70% survival rate and there is hope that the reintroduction can eventually be a success (Manvell & Goriup 2017).

The Great Bustard translocations have begun to restore bustard populations to parts of their range where they were extirpated. However, the translocated populations are small, slow-growing, suffer high levels of mortality, and are unlikely to expand far outside of the areas where they were released because they are surrounded by land
under hostile agricultural practices. They were not intended to have global-level population impacts, and they are unlikely to do so because large populations of Great Bustard persist elsewhere in the species range. They do, however, highlight the difficulties associated with reintroducing bustards, even when the reintroduction situation has been designed to mimic closely their natural environment.

2.4.7 Captive breeding combined with population supplementation

Asian and African Houbara are the subject of the largest-scale re-stocking of a threatened bird population in the world. Since the mid early 1990’s, nearly 500,000 bustards have been bred at state of the art captive breeding facilities across North Africa, Middle East and Central Asia and released into the wild to supplement hunted populations (ECWP 2019; IFHC 2019). Captive breeding facilities are funded and managed under the umbrella of the International Fund for Houbara Conservation (IFHC), which is chaired by H. H. Sheikh Mohammed bin Zayed Al Nahyan, Crown Prince of Abu Dhabi, and the Emirates Centre for Wildlife Propagation (ECWP). Females are fertilized by artificial insemination and there is careful genetic management of captive populations. This has led to genetic changes in several life history traits including increases in male display period and ejaculate size, and increased female fecundity (Chargé et al. 2014).

Published estimates of juvenile and adult survival probability, nest success and migratory behavior of released Asian and African Houbara vary widely. Many studies lack appropriate control groups, owing to extirpation of locally relevant wild-bred
populations and the difficulty of distinguishing unmarked captive-bred and wild birds. Published data suggest that short-term post-release survival is influenced by rainfall (less is better), ambient temperature (higher is better), group size on release (bigger is better), age at release (older is better), timing of release (at least in Morocco autumn is better than spring), whether soft or hard release is used (soft is better), whether their wings are clipped or they are fully-winged (an ability to fly is better), and whether supplementary food is provided (better if it is) (Saint Jalme et al. 1996; Combreau & Smith 1998; Hardouin et al. 2014; Azar et al. 2016; Bacon et al. 2019). Captive-bred Asian Houbara show a lower survival rate than wild birds in United Arab Emirates (UAE) (Azar et al. 2016) and Uzbekistan (Dolman et al. 2018). Population recruitment rates are very low (e.g. 0.04 individuals per female) in some restocked populations (Azar et al. 2018). Breeding performance of captive-bred birds remains low relative to wild-bred birds of the same age throughout their lives (Bacon et al. 2019), although the general pattern of reproductive senescence is similar in captive-bred and wild-bred individuals (Bacon et al. 2017). Captive Asian and African Houbara lay eggs that are lower in mass and smaller in linear dimensions than those laid by wild birds, which may reduce survival of chicks and juveniles, and captive-bred adult females are up to 20% smaller, which imposes constraints on egg size because the diameter of the oviduct and pelvic opening are directly related to the size of the bird (Anderson & Deeming 2002; Bacon et al. 2019). Wild-bred and captive-bred African Houbara in Morocco occupy different areas although they exploit similar ecological niches within those areas (Monnet et al. 2015), and their diets are also similar (Bourass & Hingrat 2015). In one non-migratory population of Asian Houbara, the home-range size of captive-bred birds was approximately 30% smaller than that of wild-bred birds (Islam et al. 2013). Captive-bred migratory Asian
Houbara depart later and undergo a migration that is 30% shorter than their wild counterparts (Burnside et al. 2017).

Selection in captivity has evidently altered a range of physiological, reproductive and behavioral traits in captive bred Houbara relative to wild birds, which has led to elevated mortality rates owing to starvation, disease or predation, possibly due to differences in anti-predator behavior, foraging ability or immunity to pathogens (Dolman et al. 2018). The primary cause of adult and chick mortality in captive bustards is trauma sustained through collisions with cage architecture, and stress during handling is the major impediment to reproductive performance in birds that are bred by artificial insemination, so in captive Houbara populations there is intentional and unintentional selection for tameness, docility and reduced vigilance (Van Heezik & Ostrowski 2001; Van Heezik & Seddon 2001; Hanselmann et al. 2013). Annual survival rates of captive-bred birds increase with years since release (Azar et al. 2016). Fitness traits are heritable, so increased supplementation brings the risk of domestication of wild populations with unknown demographic consequences (Dolman et al. 2018). Captive-breeding and population supplementation has increased the number of birds that are available to be hunted, at least locally, but it has largely failed to increase the size of wild populations or prevent their ongoing declines. In Uzbekistan, where thousands of captive-bred bustards are released annually, survival rates of released birds are so low that the releases alone are insufficient to compensate for birds killed by hunting (Dolman et al. 2018). An additional concern is that re-stocking of wild Houbara populations may increase hunting opportunities, leading to density dependent impacts on wild populations that might otherwise be spared from hunting owing to the scarcity of birds (Champagnon et al. 2012). It is questionable
whether supplementation of wild Asian and African Houbara populations with captive-bred birds is a good conservation strategy, but it is unlikely to cease.

2.5 Application of lessons from global conservation of bustards to H. b. blandini

In a recent global analysis of risks to biodiversity from agricultural land-use change, Cambodia was shown to be exceptional in an Asian context because it exhibits a combination of high agricultural growth rates, low conservation funding and high potential future biodiversity loss (Kehoe et al. 2017). Bustards can thrive in agro-ecosystems but because of agricultural intensification they rarely do, whilst protected areas are often poorly designed or improperly managed from the perspective of bustard conservation. Both of these approaches to bustard conservation require high quality environmental governance, either to protect hard boundaries of protected areas that are located in places that would otherwise be farmed (land sparing) or to regulate farming methods in such a way that farming can benefit the target species (land sharing) (Kremen 2015). Unlike Europe, Cambodia has a poorly developed regulatory framework and relatively poor governance, so laws and regulations are inconsistently applied and/or adhered to (Transparency International 2017). Protected area management is generally less effective in low governance countries, and for various reasons governments find it challenging to ensure that individuals and companies adhere to regulations that restrict financially lucrative activities that damage protected areas, such as farming (Lockwood 2010). Conservation is costly (McCarthy et al. 2012), and in Cambodia and similar countries, governments either lack the funds to cover basic protected area management costs or prioritise other parts of government operations for funding (Royal Government of Cambodia 2013). Agri-environment
schemes are also financially costly when implemented at scale, for instance, although they constitute only a fraction of the budget of the CAP, agri-environment schemes account for more than half of the total money spent on conservation by European governments (Batáry et al. 2015). Agri-environment schemes also lower agricultural productivity, and only became mandatory under the CAP when it was apparent that the subsidy system was producing a costly and difficult to manage surplus of goods (Bignal 1998). In Cambodia, rice is a priority export item and increased rice production is regarded as an effective mechanism for lowering the poverty rate of rural people (Royal Government of Cambodia 2010). Significant gains have been made in this regard: the rural poverty rate has fallen by more than 50% since 1990, and the country has maintained an annual GDP growth rate of at least 6% since 2010 (Asadullah & Savoia 2018). It would be antithetical to Cambodia’s development aims (and the aims of governmental and non-governmental development agencies) for government to fund schemes that actually lower agricultural productivity, even if the relevant ministries had sufficient budget to fund such subsidies (Royal Government of Cambodia 2013).

If protected area management for bustards is ineffective and trade-offs between conservation and development mean that governments will not implement agri-environment schemes to protect bustards on farmland, then some of the responsibility for bustard conservation must fall to civil society, NGOs or the private sector. Local communities in rural Cambodia are typically poor, and therefore more concerned with short-term food and financial security, rather than issues like sustainability and bird conservation (Beauchamp et al. 2018a). NGOs could theoretically provide technical support and locally-appropriate incentives to communities at key sites to manage
farmland in a particular way that would benefit bustards, but this is only morally acceptable if incentives equal or outweigh the social and financial opportunities that people had foregone (Loos et al. 2014). In the parts of Cambodia where Bengal Florican is found, agricultural intensification is associated with a 6% increase in household wealth, so any agri-environment scheme that reduced farming intensity would have to compensate for that (Ibbett et al. 2019). As with European agri-environment schemes, uptake is critical, but farmer participation must be voluntary and, initially at least, participation is likely to be low because poor farmers are understandably risk averse (Beauchamp et al. 2018a). Moreover, incentives need to be maintained beyond the usual 3–5 year donor grant cycle within which NGOs usually operate or trust will be lost and impacts felt by neither communities nor conservation targets.

In the absence of sustainable NGO/development agency financing for agri-environment schemes, conservation practitioners may embrace a private sector led approach to changing farmer behavior (Tayleur et al. 2018). An increasing number of companies have embraced certification, or have corporate social responsibility statements that indicate a willingness or commitment to consider social and/or environmental issues in sourcing of raw ingredients (Rueda et al. 2017), although only 1.1% of global cropland is actually under certification (Tayleur et al. 2017). Farmers will typically produce whatever the private sector is willing to buy, so companies have considerable leverage over farmers, and even governments, to drive change in production practices. Although this is an avenue worthy of consideration for conservation of Bengal Florican, conservationists should be cautious because market forces may drive companies to change their priorities to ensure that they remain
profitable. Bustards need long-term change in agricultural practices, as evidenced in the example from France (Bretagnolle et al. 2018b).

If the private sector and/or government cannot be relied on to provide suitable incentives to farmers on a timescale that is needed for bustard conservation, then an alternative option for conservationists is to become the private sector. In Cambodia, WCS established a company, Ibis Rice Conservation Company Ltd (Ibis Rice), to do just that in areas of northern Cambodia where farmers that live in protected areas were clearing habitat that was vital for the Critically Endangered Giant Ibis *Thaumatibis gigantea*. Ibis Rice purchases rice at a price premium from farmers who adhere to regulations that prohibit clearing of forest, hunting and use of chemicals. This rice is then sold as a boutique product and the company is profitable (WCS unpublished data). Deforestation rates in villages where Ibis Rice is grown are lower than in areas where it is not, and Ibis Rice farmers are wealthier and have a better standard of living than their compatriots (Clements et al. 2010; Clements et al. 2013; Beauchamp et al. 2018b, 2018a). The main challenge to replicating a system like this in an area that is important for Bengal Florican is achieving the necessary scale in both farmer uptake and market sales.

2.5.1 Summary

The conservation of bustards is extremely challenging owing to their physical and ecological characteristics. Bustards face threats that are common to many groups of birds, but they are especially heavily impacted by agricultural intensification and
hunting. Several management approaches have been trialed, but none have been an unequivocal success. The Cambodian population of Bengal Florican is particularly heavily threatened, and to have a chance at preventing its extinction conservationists will need to act quickly.

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Chapter 3.

Catastrophic ongoing decline in Cambodia’s Bengal Florican

*Houbaropsis bengalensis* population

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Key words

Agricultural intensification, Bustard, Grassland, Preventing extinction, Traditional agriculture

Abstract

In 2013 a prediction was made that the Southeast Asian subspecies of Bengal Florican *Houbaropsis bengalensis blandini* would be extinct within ten years. In 2018 we conducted a survey in the Tonle Sap floodplain, Cambodia, of the last population of Bengal Florican in Southeast Asia. We found that the rate of decline in displaying males was 55% over five years, a decline comparable to that recorded between 2005-2007 and 2012. The estimated number of displaying males in 2018 was 104 (95% CI: 89–117), down from 216 (95% CI: 156–275) in 2012. We also conducted surveys by flushing birds in the non-breeding season, which indicated that the sex ratio of males to females is 3:1. We therefore estimate that the total population of adult Bengal Floricans in Cambodia in 2018 was 138 (95% CI: 119–156), making *H. b. blandini* the most threatened bustard taxon. The number of sites that support displaying male Bengal Floricans was reduced from ten to four between 2012 and 2018. Between 2012 and 2018 we monitored numbers of displaying males in most years at the sites that support 80% of the total population. The only site where numbers of birds are stable is Stoung-Chikraeng Bengal Florican Conservation Area, where there were 44 (95% CI: 25–63) displaying males in 2018. This is the only site that has an ongoing NGO-government conservation program. Our data indicate that Bengal Floricans are lost from sites when the area of grassland falls below 25 km². We found evidence that displaying male Bengal Floricans abandon display territories when grassland is lost, this also creates hope that they may disperse and could colonize newly created habitat.
All remaining sites that support Bengal Floricans in Cambodia are imperilled and we outline what must be done to reduce the possibility that *H. b. blandini* will be extinct by 2023.

**Introduction**

The bustards of Asia are one of the most threatened groups of birds worldwide (Collar et al. 2017). Of the six species recorded in the region, all are considered globally threatened or Near Threatened, two are Critically Endangered and one Endangered (BirdLife International 2018). Of the two Critically Endangered species, the Bengal Florican *Houbaropsis bengalensis* is polytypic with *H. b. bengalensis* confined to protected areas in floodplain and alluvial grasslands in north-east India and Nepal and *H. b. blandini* now restricted to the Tonle Sap floodplain of Cambodia, although it formerly also occurred in the Mekong Delta (Collar et al. 2018). Rice has been cultivated in the Tonle Sap floodplain for at least 1,000 years (Vanna 2002). Between the 9th and 15th century, rice cultivation was sufficiently intensive that a surplus was produced to feed the workers building Angkor Wat, the world’s largest religious building (Campbell et al. 2006). This rich-ethno cultural landscape was characterised by cultivation of deep-water rice varieties, which were grown during the flood season on fields that are left fallow when floodwaters recede, coupled with patches of grassland maintained through traditional burning and grazing regimes (Gray et al. 2007). These traditional agricultural practices inadvertently replicated the processes of long extinct ungulate populations, creating ideal habitat for Bengal Florican (Gray et al. 2007). Like all bustards, Bengal Floricans are terrestrial, and require large expanses of relatively flat, open habitat to enable them to spot predators, and so that
their courtship displays can be seen from great distance (Collar et al. 2018). Females
nest on the ground in patches of denser vegetation, and after breeding both sexes
migrate up to 60 km annually to escape rising floodwaters (Gray et al. 2009b;
Packman 2011). The Bengal Florican has little cultural significance to the people of
Cambodia (Goes 2013), but for at least a millennium its fate has been closely tied to
agricultural practices of the communities living in the Tonle Sap floodplain, the rice
bowl of Cambodia.

Following decades of conflict, Cambodia’s Bengal Florican population was
rediscovered in 1999, and market-driven hunting was quickly identified as the most
significant threat (Goes 2013). This was addressed through rapid conservation action,
focusing on raising awareness of communities and law enforcement personnel
(Davidson 2004). As hunting pressure was reduced, conversion of grassland and low
intensity agriculture to intensive dry-season rice rapidly emerged as a new and highly
pertinent threat (Packman et al. 2013a). Grassland cover in the Tonle Sap floodplain
decayed from 3,349 km² to 1,817 km² between 1995 and 2005, and grassland loss has
subsequently continued owing to a massive and sustained expansion in dry-season
rice production driven by expansion of irrigation infrastructure (Packman et al.
2013a). As well as causing direct loss of Bengal Florican habitat in the outer
floodplain, construction of irrigation infrastructure physically blocked the seasonal
migration routes used by cattle herders, leading to a 23% increase in scrub cover at
the expense of the rich inner floodplain grassland between 1995 and 2005 (Packman
et al. 2013a). Irrigation and concomitant mechanization have enabled farmers to
convert almost all remaining areas of grassland to agriculture and switch from
cultivating deep-water rice to dry-season rice. Initially irrigation infrastructure was
constructed to service concessions granted to wealthy businessmen (Gray 2008). However, even close to sites that retained Bengal Florican, by 2005 dry-season rice was cultivated by one third of villages, and by 2012 it was ubiquitous (Ibbett et al. 2019). Farmers prefer the taste of deep-water rice and consider it healthier than modern varieties, but yields are tied to the extent and duration of the flood, which they perceive as becoming increasingly variable (Ibbett et al. 2019). Irrigation allows farmers to control water levels, and the switch to dry-season rice is indeed associated with an increase in household income, although farmers do not like the heavy chemical use associated with dry-season rice and rarely keep it for home consumption (Ibbett et al. 2019).

Sites that supported large Bengal Florican populations in the early 2000s, such as Sankor and Koup Prea Bueng Trea (see Figure 1 for locations of sites), were converted to dry-season rice relatively early in the 21st century. The limited scale of early irrigation infrastructure permitted only a single crop of dry-season rice per year, which was harvested early in the breeding cycle of the Bengal Florican (WCS unpublished data). Although Bengal Floricans typically avoid dry-season rice cultivation (Gray et al. 2009b), fallow fields and vegetated head-ponds that dried out after one crop of dry-season rice make suitable (although potentially sub-optimal) breeding habitat for Bengal Florican (Son Virak pers. obs.). Recent improvements to irrigation infrastructure mean that these areas can now support two or even three crops of dry-season rice each year, so they and the head ponds that feed them remain flooded until much later in the breeding cycle of Bengal Florican (Ibbett et al. 2019). Since Bengal Floricans nest on the ground, this change in agricultural practices
reduces or even eliminates the amount of time when there is habitat suitable for nesting or for the rearing of chicks.

**Figure 1.** Map of the Tonle Sap floodplain showing sites where Bengal Florican monitoring has been conducted since 2005–2007 (see Table 1 for site codes). Shading indicates most recent census year when each site supported displaying males.

In response to the loss of much of the grassland, the first grassland reserves (Integrated Farming and Biodiversity Areas: IFBAs), totalling 349 km², were established under provincial declarations in 2007 with the aim of preserving favourable agricultural systems (Gray et al. 2009b). Legal protection of these sites was improved in 2010 under a decree from the Ministry of Agriculture Forestry and
Fisheries that established Bengal Florican Conservation Areas (BFCAs) (Packman et al. 2013b). However this came at a cost because the area of floodplain breeding habitat under protection was reduced to 173 km² (four sites constituting two management units), although an additional 138 km² of non-breeding habitat outside of the floodplain (two sites) was added to the protected area network. By this time there were already large rice concessions within Chikraeng and Chong Duong BFCAs which could not be cancelled. Although there was an agreement that these would at least not be expanded, this commitment has not been adhered to (Mahood et al. 2012). In 2016 the six BFCAs were combined into one management jurisdiction under a prime ministerial sub-decree, the highest level of legal protection, which re-named them the Northern Tonle Sap Protected Landscape (for ease of reference the individual sites are still referred to as BFCAs). Field conservation of Bengal Floricans by Wildlife Conservation Society (WCS) in collaboration with the Ministry of Environment has focussed on community-based management on Stoung-Chikraeng BFCA for historical, ecological and logistical reasons.

In Cambodia a complete census of all 19 areas that supported suitable Bengal Florican habitat in 2005 (suitable habitat was identified using aerial photographs) was conducted between 2005 and 2007, yielding an estimate of 416 (95% CI 333–502) displaying males at eleven sites (Gray et al. 2009a). The census was repeated in 2012, when a total of 216 (95% CI 156–275) displaying males was estimated at ten sites out of 20 surveyed (Packman et al. 2013b). Owing to an absence of information to the contrary the sex ratio was assumed to be equal and the total Cambodian population was estimated to be 432 (95% CI 312–550) individuals (Packman et al. 2013b). After correcting for differences in survey methodology, the estimated population decline in
Cambodia between the two censuses was 44–64%. *H. b. blandini* was predicted to be extinct within ten years i.e. by 2023 (Packman et al. 2013b). Given this dire prediction, we consider it important to provide an up-to-date assessment of the status of the total Bengal Florican population in Cambodia at the mid-point of that period, to test whether management of the habitat has been effective in stemming declines. We have also analysed population and habitat data collected over the past five years to help understand recent population trends and make conservation recommendations for the Bengal Florican and other imperilled Asian bustards.

**Methods**

The Bengal Florican is extremely cryptic except during the breeding season, when males perform display flights and strut around with puffed out neck feathers (Collar et al. 2018). Bengal Florican has an exploded lek breeding system, >4 males are required for a lek to function (Gray et al. 2007) and each male needs up to 2.5 km\(^2\) of habitat from which to display (Gray et al. 2009b; Packman 2011), so conservatively only sites >10 km\(^2\) in 2005 were considered for survey (Gray et al. 2009a). Locations of the sites are shown in Figure 1, and sizes in Table 1. Of the 20 sites visited in 2012 (19 in 2005–2007), only 13 were visited in 2018 (Table 1). The six sites not visited in 2018 comprised four sites where no Bengal Florican was recorded during either previous survey (i.e. there have been no records since pre-2005), as well as two former breeding sites located outside of the Tonle Sap floodplain: Mongkol Borei where no bird was recorded during 2013 or in subsequent casual visits, and Ang Trapeang Thmor where there has been just one record since 2012 despite intensive survey effort. It was assumed that floricans no longer use these sites, or that if they do
so, populations are likely to be too low for a functioning lek to persist. Six sites in the southeast of the Tonle Sap floodplain were also surveyed in most years between the 2012 and 2018 censuses, although no sites were surveyed in 2015 due to logistical reasons (Table 1).

**Table 1.** Survey sites, their area, and frequency of survey.

<table>
<thead>
<tr>
<th>Site (with codes)</th>
<th>Site area (Km²)</th>
<th>Years in which surveys were conducted</th>
</tr>
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<tbody>
<tr>
<td>Baray District (BD)</td>
<td>258</td>
<td>Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y</td>
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<tr>
<td>Chong Duong (CD)</td>
<td>34</td>
<td>Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y</td>
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<tr>
<td>Kouk Preah Beung Trea (KP)</td>
<td>216</td>
<td>Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y</td>
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<tr>
<td>Kruos Kraom (KK)</td>
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<td>Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y</td>
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<tr>
<td>Veal Srangei (VS)</td>
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<td>Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y</td>
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<tr>
<td>Sankor (SK)</td>
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<td>Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y</td>
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<tr>
<td>Stoung-Chikraeng (SC)</td>
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<td>Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y</td>
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<tr>
<td>Puok Lvea (PL)</td>
<td>43</td>
<td>Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y</td>
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<tr>
<td>Ang Trapeang Thmor (AT)</td>
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<td>Site (with codes)</td>
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<td>Mongkol Borei (MB)</td>
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<td>Aek Phnum (AP)</td>
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<td>Bavel (BV)</td>
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Numbers of displaying male Bengal Florican have been monitored almost annually in the floodplain BFCAs and the other four sites located in the southeast of the Tonle Sap floodplain. In 2012 these supported 79% of the Cambodian population (Packman et al. 2013b). Annual monitoring and the 2018 total population census followed the same methods used in 2012, as detailed in (Packman et al. 2013b). They are
summarized here. Population estimates at sites were derived from sampling using 1 km$^2$ replicate squares, each separated by 1km, laid in a grid over each site (survey squares are regularly spaced not randomly selected to maximise the number of survey squares at each site). Surveys aimed to sample a minimum of 20% of the area of each site with a minimum of eight survey squares per site. Within each square, the number of displaying male Bengal Floricans was recorded over two separate one hour periods by two different observers during the period of peak male display activity (first and last two hours of day). Visits were conducted between mid-March and mid-May, the period of peak Bengal Florican display activity. During the 2018 census 162 survey squares were visited twice with the maximum of the two counts of displaying males used for population estimation. An additional 40 survey squares could not be visited because they were either flooded or filled with dense scrub so their Bengal Florican population was assumed to be zero.

For each site, mean density of displaying males was calculated by dividing the maximum count of displaying males in each square by the total number of squares. This number was then multiplied by the area of the site to give a population estimate. In calculating the overall population estimate, sites were treated as strata to account for unequal survey effort among sites following (Gray et al. 2009a) such that population estimates from sites were summed, whilst confidence intervals were calculated as the square root of the sum of site level variance. Because we used exactly the same survey method as (Packman et al. 2013b), we were able to evaluate differences between population estimates in 2012 and 2018 using the Z-test. Analysis was conducted in R version 3.5.1 (R Core Team 2018). The number of displaying males in a given survey square was typically 1 or 0, so we used an occupancy
framework to estimate detectability, comparing the numbers of Bengal Floricans located during just the first or just the second visit to the maximum count recorded across both visits.

From 2013 onwards, area of habitat was visually estimated in visited survey squares in the following broad categories: grassland, rice, scrub, water and other. There was a total of 1,639 square/site/year habitat data points. These data were used to calculate area of grassland within each survey square in each year that it was visited, and mean grassland cover within squares was multiplied by the area of the site to estimate grassland cover within the site. We conducted linear regressions with site as a fixed factor to examine the relationship between site-level Bengal Florican populations and grassland loss and we conducted logistic regression to evaluate impacts of habitat change on Bengal Florican presence/absence in survey squares. All analyses were conducted using R (R Core Team 2018).

During the breeding season male Bengal Floricans flush easily, whilst females sit tight and flush only at very short range. To investigate the sex ratio of Bengal Floricans we conducted surveys between 2011 and 2017 during the non-breeding season, when floricans are more likely to be equally cryptic. During the non-breeding season when the floodplain is inundated, the Bengal Floricans migrate to degraded deciduous forest up to 60 km beyond the breeding grounds (Packman 2011; Hillard 2012). Males and females are cryptic when not breeding, so birds were flushed by a line of three or four observers walking through the habitat, with each person separated by 10-20 meters. Any Bengal Floricans flushed by the team were sexed, and the
distance measured from the observers to the location where the bird had flushed. A t-test was used to evaluate whether there was a difference between flushing distances of male and female Bengal Floricans.

Results

The total population of Bengal Florican in Cambodia in 2018 was estimated as 104 (95% CI: 89–117) displaying males (Figure 2). This indicates that the population has declined by 52% since 2012 when the total number of displaying males was estimated as 216 (95% CI: 156–275) (Packman et al. 2013b). This is equivalent to an annual rate of decline of 8.6%, which is largely unchanged since 2005–2012. The area of grassland in surveyed squares declined by 10.9% per year between 2013 and 2018. Detectability during the 2018 survey was extremely high, single visits recorded 81% of the maximum number of displaying males detected over two visits, so the population estimate is probably accurate. Although females are more cryptic than displaying males during the breeding season, data gathered during the non-breeding season over 115 team/days found no statistically significant difference in flushing distance between the sexes (one-sample t (85) = -1.714, p = 0.090), although two males flushed at a much greater distance than any of the females (Figure 3). Of the 88 Bengal Floricans recorded between 2011 and 2017 during surveys conducted at non-breeding sites, a ratio of three males to one female was observed. This ratio indicates that there may only be 34 (95% CI: 30–39) females remaining in Cambodia. The total population (excluding non-displaying males) is therefore estimated at 138 (95% CI: 119–156).
Figure 2. Estimates of total population (with 95% CI) of displaying male Bengal Florican in Cambodia.

Figure 3. Flushing distance of Bengal Florican in the non-breeding season (n = 88, Females = 22, Males = 66; grey box indicates 95% CI around mean, vertical line indicates range and black dot is an outlier).
Displaying male Bengal Floricans were detected in only four sites during the 2018 census compared to ten in 2012 and eleven in 2005–2007 (Table 2). A small number of non-displaying male Bengal Floricans were recorded at one additional site (Koup Prea Bueng Trea). Bengal Floricans have now been extirpated from all except one of the sites located outside of their core range in the southeast of the Tonle Sap floodplain, and that site, Bakan, located in the southwest of the floodplain, is estimated to support only 3 (95% CI: 0–11) displaying males at a density of 0.14 displaying males/km². Of the other sites that still support displaying male Bengal Florican in 2018, nearly half the birds were found in one relatively small protected area where the population is stable: Stoung-Chikraeng BFCA. At that site the population is estimated at 44 (95% CI: 25–63) at a density of 0.59 displaying males/km². Baray District (a relatively large site encompassing Baray BFCA and unprotected grassland to the east) now supports one third of the total population: 36 (95% CI: 5–37) at a density of 0.14 displaying males/km². Population trends at Baray District are unclear and the change between 2012 and 2018 was non-significant (Figure 4). The population at Sankor, a large unprotected site that supported the largest population in 2005–2007 (87; 54–120), underwent a statistically significant decline between 2012 and 2018 to just 21 (0–44) displaying males (Z = 1.66, p = 0.048; Figure 4). Displaying males at Sankor now occur at a density of 0.13 displaying males/km².
Table 2. Estimated numbers of displaying males by site (with 95% CIs) for censuses conducted in 2005, 2006 or 2007 (Gray et al. 2009a), 2012 (Packman et al. 2013b) and 2018; % population change (2012–2018) with significance (Z-test: **p<0.005, *p<0.05, NS p>0.05).

<table>
<thead>
<tr>
<th>Site</th>
<th>Estimated number of displaying males (95% CI)</th>
<th>Percent change 2012–2018</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2005–2007</td>
<td>2012</td>
</tr>
<tr>
<td>Baray District</td>
<td>65 (19–199)</td>
<td>18 (0–37)</td>
</tr>
<tr>
<td>Chong Duong</td>
<td>12 (0–26)</td>
<td>0</td>
</tr>
<tr>
<td>Kouk Preah Beung Trea</td>
<td>53 (20–86)</td>
<td>54 (16–92)</td>
</tr>
<tr>
<td>Kruos Kraom</td>
<td>17 (9–26)</td>
<td>0</td>
</tr>
<tr>
<td>Veal Srangei</td>
<td>16 (4–28)</td>
<td>2 (0–5)</td>
</tr>
<tr>
<td>Sankor</td>
<td>87 (54–120)</td>
<td>53 (22–83)</td>
</tr>
<tr>
<td>Stoung-Chikraeng</td>
<td>49 (40–59)</td>
<td>43 (20–66)</td>
</tr>
<tr>
<td>Puok Lvea</td>
<td>11 (0–26)</td>
<td>5 (0–16)</td>
</tr>
<tr>
<td>Ang Trapeang Thmor</td>
<td>-</td>
<td>5 (0–15)</td>
</tr>
<tr>
<td>Preah Net Preah</td>
<td>16 (4–29)</td>
<td>11 (0–33)</td>
</tr>
<tr>
<td>Mongkol Borei</td>
<td>38 (0–88)</td>
<td>0</td>
</tr>
<tr>
<td>Thmor Kol</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Aek Phnum-Preak</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Aek Phnum</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Bavel</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Site</td>
<td>Estimated number of displaying males (95% CI)</td>
<td>Percent change 2012–2018</td>
</tr>
<tr>
<td>-----------------------</td>
<td>-----------------------------------------------</td>
<td>-------------------------</td>
</tr>
<tr>
<td></td>
<td>2005–2007</td>
<td>2012 (0–24)</td>
</tr>
<tr>
<td>Sangkae-Kampong Pring</td>
<td>12 (6–18)</td>
<td>12 (0–24)</td>
</tr>
<tr>
<td>Moung Russei</td>
<td>0 (0–24)</td>
<td>0 (0–24)</td>
</tr>
<tr>
<td>Koas Kroala</td>
<td>0 (0–24)</td>
<td>0 (0–24)</td>
</tr>
<tr>
<td>Bakan</td>
<td>0 (0–24)</td>
<td>14 (6–21)</td>
</tr>
<tr>
<td>Kandieng</td>
<td>0 (0–24)</td>
<td>0 (0–24)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>376 (293–462)</td>
<td>216 (156–377)</td>
</tr>
</tbody>
</table>

Figure 4. Site-specific trends in displaying male Bengal Floricans in the core Cambodian breeding range (dashed lines bridge years with no population census, whiskers are 95% CIs around population estimates).
Small sites historically supported the highest densities of Bengal Florican (Gray et al. 2009a). In 2018, relatively small sites continue to hold the highest densities of displaying male Bengal Floricans, and as the total population has declined, the relative importance of small sites has increased. Nonetheless, most of the sites with the highest density of floricans in 2012 now support none (e.g. Sangkae Kampong Pring). Numbers at larger sites with lower densities have also declined rapidly (e.g. Sankor), or been lost entirely over the last six years (Table 2).

Near-annual monitoring of Bengal Florican and habitat in the southeastern subset of sites revealed that the area of grassland in a site in the previous year has a stronger influence on population size than area of grassland in the year of the population census ($Y_0$: $F(6, 19) = 9.15, p < 0.001, R^2 = 0.66$; $Y_{-1}$: $F(6, 5) = 11.82, p < 0.008, R^2 = 0.86$). Moreover, when there was less than 25 km$^2$ of grassland at a site, displaying males were no longer recorded (Figure 5). The one exception to this is the data from Sankor in 2018, where a population of 21 (95% CI: 0–44) displaying males was estimated (Table 2). However, the area of grassland in Sankor was still high in 2017 (57 km$^2$), declining catastrophically to 9.6 km$^2$ in 2018 when the birds may simply have been returning to areas that had been grassland in the previous year. The presence or absence of a displaying male Bengal Florican within a given survey square was not influenced by the area of grassland within the site where the square was located (Table 3). However, male Bengal Floricans were more likely to display from survey squares that contained a greater area of grassland, although the probability of a male displaying in a square was unrelated to the amount of grassland in previous years (Table 3).
**Figure 5.** Relationship between area of grassland in a given site and a given year and the number of displaying male Bengal Floricans at that site in that year (data span 2013–2018 and were collected at sites in the core Cambodian breeding range).

**Table 3.** Logistic regression of Bengal Florican occurrence in survey squares between 2012 and 2018 in the southeast floodplain (data from different years and sites are pooled)

<table>
<thead>
<tr>
<th>Predictor</th>
<th>β</th>
<th>SE β</th>
<th>Wald’s $X^2$</th>
<th>df</th>
<th>p</th>
<th>$e^\beta$ (odds ratio)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-2.289</td>
<td>1.696</td>
<td>-1.350</td>
<td>1</td>
<td>0.177</td>
<td>NA</td>
</tr>
<tr>
<td>Grassland area (site)</td>
<td>0.094</td>
<td>0.471</td>
<td>0.199</td>
<td>1</td>
<td>0.842</td>
<td>1.098</td>
</tr>
<tr>
<td>Grassland area (square; Year 0)</td>
<td>0.014</td>
<td>0.005</td>
<td>2.275</td>
<td>1</td>
<td>0.006**</td>
<td>1.014</td>
</tr>
<tr>
<td>Grassland area (square; Year -1)</td>
<td>0.007</td>
<td>0.005</td>
<td>1.569</td>
<td>1</td>
<td>1.569</td>
<td>1.007</td>
</tr>
</tbody>
</table>
Discussion

In 2013 it was predicted that the Bengal Florican could be extinct in Cambodia within ten years, based on the rate of decline between 2005–2007 and 2012 (Packman et al. 2013b). Five years later the results of the 2018 census indicate that the rate of decline has remained constant, meaning the prognosis for the population is still dire. Rate of grassland loss in survey squares is only slightly higher than the rate of decline in the Bengal Florican population, affirming the notion that grassland loss caused by agricultural intensification is the greatest threat to Cambodia’s Bengal Florican population. Our data confirm that males return to display in territories that supported suitable habitat in the previous breeding season (Packman 2011), but that they will not continue to display in squares that no longer contain suitable habitat for attracting a mate. This indicates a degree of home-range plasticity that was suspected but not previously confirmed. It offers hope that birds dispersing from habitat that has been destroyed may colonize new sites if suitable habitat is created, and they could potentially use seasonal fallows within a rotational farming system. Our results suggest a minimum threshold grassland area of approximately 25 km² for persistence of a functioning exploded lek of Bengal Florican (Figure 5), a significantly larger area than was previously suspected (Gray et al. 2009a). Satellite telemetry has indicated that, although male floricans display within a relatively small area (1.6 ± 0.3 – 2.6 ± 0.9 km²), they use an area at least ten times larger during the breeding season (Packman 2011). In this context, it is unsurprising that no Bengal Floricans were recorded in 2012 or 2018 at some of the smaller sites, nor that birds were lost from
almost all of the small sites between 2012 and 2018. Of the four sites that still support
Bengal Florican populations, only Baray District and Stoung-Chikraeng BFCA still
contain more than 25 km² grassland. Population estimates and trajectories in these
two sites vary greatly (Figure 5), indicating that factors other than grass cover also
influence population size. Non-breeding season habitat loss has been more severe in
the area used by Bengal Floricans from Baray District than in the area used by the
birds that breed in Stoung-Chikraeng BFCA and Sankor, which is protected as Trea
Sameakki BFCA. Sub-optimal non-breeding habitat may lead to reduced breeding
success in migratory birds (Norris et al. 2004) and this may be true for Bengal
Florican for which conditions in much of the area used during post-breeding dispersal
are hostile (Newton 2006).

The sex ratio recorded in Cambodia’s Bengal Florican population is a cause for
concern because highly male-skewed sex ratios are typically associated with declining
populations (Donald 2007). In most adult bird species, males outnumber females by
2:1, although there may be a tendency towards female-biased sex ratios in lekking
birds (Donald 2007). It was not possible to test for differences in the sex ratio between
breeding sites, because surveys to investigate sex ratios were undertaken in the non-
breeding season when birds are usually absent from breeding sites. Satellite telemetry
indicates that female Bengal Floricans spend more time in the non-breeding grounds
than males (Packman 2011), which would make them more likely to be encountered
during surveys of the non-breeding grounds. Unlike some other bustard species there
is no evidence that in Bengal Florican the sexes differ in their choice of non-breeding
habitat or location (Hillard 2012) in a way that might have affected detectability in
our survey. Nonetheless, our estimate of the sex ratio in Cambodia’s Bengal Florican
population should be considered provisional owing to the possibility that it is influenced by an unknown source of bias.

The apparent skewed sex ratio is probably caused by relatively high female mortality, because sex-biased survival is a strong predictor of adult sex ratios in birds (Székely et al. 2014). There are a number of plausible causes of elevated female mortality in Bengal Floricans. Many local people work in or travel through the areas where Bengal Floricans breed, when people locate a ground-nesting bird’s nest the female is traditionally snared at the nest before the egg is taken (C. Hong pers. obs.). Although estimated annual survival rates are comparable to other bustards (89.9% 82.2–97.6%) (Mahood et al. 2016), small-scale local hunting may still occur at such a low rate that it is impossible to detect (Ibbett et al. 2019). Free-ranging domestic dogs, which are a problem for many species (Doherty et al. 2017) including bustards (Collar et al. 2015), might also be significant predator of nests and incubating females. Chewed feathers from a female Bengal Florican have been found at a failed nest site (S. Mahood and Son Virak pers. obs.). Conversely, mechanization (which is positively associated with rural to urban migration) and a lack of access for cattle and their attendant herders may have incidentally reduced hunting levels at intensively farmed sites because there are now fewer people in the farmland.

With an estimated total population of just 138 (95% CI: 119–156) adults, the blandini subspecies of Bengal Florican is now the rarest bustard taxon globally, and must now rank as one of the most at-risk bird taxa in the world. The population is very likely to contain an unknown number of non-displaying males, whose inclusion would increase
the population estimate. We are unable to quantify the number of males in the population that were not displaying at the time of the survey, because any non-displaying males seen may or may not have been birds that were recorded displaying in other survey squares. We have been unable to trace any comparable estimates of non-displaying male bustards as a proportion of total population. Nonetheless, the population estimate for the number of displaying male Bengal Florican in Cambodia in 2018 is comparable with that derived in 2005–7 and 2012, and it is therefore at least an accurate indication of population trends, even if it is not a precise estimate of the total male population. Below we detail site-specific threats and conservation activities for all of the remaining subpopulations.

The stable Bengal Florican population at Stoung-Chikraeng BFCA superficially represents the best chance for persistence of the subspecies. The density of displaying male Bengal Florican in Stoung-Chikreang BFCA is 4x that found in the other sites that still support the species. In contrast to other sites, Stoung-Chikraeng BFCA has been the focus for a joint Wildlife Conservation Society (WCS) – Ministry of Environment community-based conservation program since 2005 (prior to 2016 the collaboration was with the Forestry Administration). Management of Stoung-Chikraeng BFCA is by a Community Management Committee, and activities include patrolling to prevent, detect and reverse grassland encroachment, a nest protection program that pays community members for successful fledging of Bengal Florican nests, and an ecotourism scheme in which sightings of the Bengal Florican are linked to payments into a community fund that has been used to build toilets at the village school, repair the pagoda and purchase medicines. In the rice growing areas used by Bengal Floricans from Stoung-Chikraeng BFCA in the non-breeding season, a
collaboration between WCS, local NGO Sansom Mlup Prey (SMP) and Mars Foods (a large-scale rice buyer) uses the Sustainable Rice Platform as a framework to test farming methods that create suitable habitat for Bengal Floricans and reduces chemical inputs, through land-levelling (which reduces the need for pesticides and herbicides) and carefully selected cover crops. Stoung-Chikraeng BFCA is evidence that it is possible for an NGO-Government collaboration to stabilize trends in a population of a Critically Endangered bird in a challenging context. The Bengal Florican is being promoted as a source of pride in Kampong Thom Province where Stoung-Chikraeng BFCA and the southeastern populations are located, and an event celebrating the species was attended by more than 200 people in 2018. To mark the event, huge billboards depicting the species were erected alongside the main road, and photographs of Bengal Florican now hang in the office of the Kampong Thom Provincial Governor and in the office of the Ministry of Environment in Phnom Penh. The conservation program at Stoung-Chikraeng BFCA costs approximately US$100,000 per year. Financial constraints have prevented expanding this successful program to Baray BFCA.

In the context of the successful conservation efforts described above, it is unfortunate that a high voltage power transmission line is currently under construction along the northern edge of the Tonle Sap floodplain, extremely close to Stoung-Chikraeng BFCA. All of Cambodia’s Bengal Florican will need to traverse the power line at least twice each year on their annual migration. Additionally, at Stoung-Chikraeng BFCA it is located close to an important lek and is predicted to significantly increase adult male mortality (Mahood et al. 2016). Even if technically feasible, financial considerations ruled out burying the power line to prevent bird collisions. Although
Electricité du Cambodge have agreed to install bird flight deflectors on the stretch closest to Stoung-Chikraeng BFCA, collisions are still highly likely (Mahood et al. 2016). The construction of the power line could therefore end breeding at Stoung-Chikraeng BFCA and increase mortality in other populations. Given the potential for colonization of newly created grassland, there is an urgent need to identify and rehabilitate abandoned or unproductive agricultural land near Stoung-Chikraeng BFCA to draw Bengal Floricans away from the area close to the power line.

The Bengal Florican population at Sankor is relatively large, but low density and declining rapidly. Sankor is unprotected, and already under intensive dry-season rice cultivation. In Sankor, WCS and SMP are investigating the appetite of AMRU (Cambodia’s largest rice exporter) and Mars Foods to mandate farmers to grow rice on rotation with fallows and a leguminous cover crop, an approach that would maintain soil quality and create habitat for Bengal Floricans. This potential intervention builds on the SRP pilot in the non-breeding grounds of the Bengal Floricans from Stoung-Chikraeng BFCA. Our results suggest that Bengal Floricans will move if habitat becomes unsuitable and fields are smaller than Bengal Florican display territories, therefore we theorize that the birds will be able to shift between fallow fields if they are created in a patchwork fashion. Moreover, other bustard species will breed successfully in young rotational fallows (Morales et al. 2013), and legumes have previously been used as a tool to reverse bustard declines (Bretagnolle et al. 2011). If these proposed measures are not acceptable to farmers or rice buyers, they fail to create suitable habitat for Bengal Floricans or if they are implemented slowly, then the species is likely to abandon Sankor within a few years.
The Bengal Florican population in Baray District is located mostly to the south-east of the BFCA, in an area that is currently too distant from irrigation infrastructure to be converted to dry-season rice. However, there are plans to construct irrigation infrastructure to the east of Baray BFCA in 2019-21, which, if not very carefully managed and potential impacts mitigated, may lead to the extinction of Bengal Florican in this site. In this context, sensitive development is critical, and there is an opportunity to promote a combination of protected area management similar to that employed at Stoung-Chikraeng BFCA, and private-sector led farming following the principles of the Sustainable Rice Platform, to give this Bengal Florican population a chance to thrive.

In Bakan WCS are working with the Ministry of Environment to establish a protected area. At the same time, local NGO SMP are promoting cultivation of deep-water rice and developing a niche agricultural product that will provide financial incentives to farmers to grow this low GI rice strain. Even if these actions are too late for this tiny population of Bengal Florican, Bakan is the best remaining example of inner floodplain grassland in the Tonle Sap floodplain and supports a suite of species that make it worth protecting regardless of the presence of Bengal Florican. Compared to other sites in the Tonle Sap floodplain, Bakan still supports large numbers of grassland passerines, including the largest wintering population of Critically Endangered Yellow-breasted Bunting *Emberiza aureola* in Cambodia, and is one of only two known locations with a population of Chinese Grassbird *Graminicola striatus* in Southeast Asia (Eaton et al. 2014).
We cannot rule out the possibility that there is a small number of Bengal Floricans in agricultural areas that we did not survey, but there is no reason to suggest that these undiscovered birds are even close to equal in number to those that are unaccounted for since 2012. Although it is plausible that Bengal Floricans disperse when grassland is destroyed, ongoing analysis of satellite images indicates that there are no large unsurveyed patches of grassland in the Tonle Sap floodplain that they could colonise. The only recent record of *H. b. blandini* outside the Tonle Sap floodplain was a female with chick in August 2015 at Bueng Prek Lapouv close to the international border with Vietnam (J. C. Eames pers. comm.). This was the first record in the Mekong Delta for a number of years, despite frequent visits to Bueng Prek Lapouv and the nearby Anlung Pring Sarus Crane Conservation Area since the mid 2000’s as part of an ongoing conservation project by BirdLife International and WWT. In the mid-2000s the population at Bueng Prek Lapouv was estimated at 2–3 displaying males (Gray et al. 2009a). There appear to have been no records of Bengal Florican from Vietnam since the late 1990’s (Donald et al. 2013). Although the recent Bueng Prek Lapouv record suggests that small numbers of Bengal Floricans can persist unnoticed for many years, the Mekong Delta population is evidently likely almost extirpated.

Given the small size of Cambodia’s Bengal Florican population and the situation at the sites outlined above, captive breeding has been suggested as a solution. However, we caution that demographic modelling, or at least a thorough evaluation of potential impacts on wild populations and possible outcomes of captive breeding, is a pre-
requisite before embarking on a long and expensive program of ex-situ conservation for a species that has never been kept in captivity (Dolman et al. 2015). Although desirable, it has not been possible to increase the size of existing BFCAs, designate additional BFCAs or purchase agricultural land and convert it to grassland (Packman et al. 2013b). Land prices in the Tonle Sap floodplain are very high so millions of dollars would be needed to purchase enough for a small grassland reserve. Furthermore, land tenure is not secure so understandably investors cannot be found. Also converting agricultural land that produces food for local consumption or export to unproductive grassland goes against Cambodia’s Rectangular Strategy, which guides sectoral policy and prioritizes economic growth (Royal Government of Cambodia 2013). Bengal Florican conservation must be implemented in the context of the development and management of the Tonle Sap floodplain, within which more than 2 million people live. The rapidly changing economic needs of these people, as well as the predicted impacts of climate change and hydropower dams on vegetation and farming (Arias et al. 2012; Arias et al. 2014), must be taken into account when designing and implementing conservation measures. In this context the only hope for Bengal Florican populations outside of the BFCAs lies in working with the private sector to incentivize farmers to grow rice in a way that enables Bengal Florican to persist. Given the area requirements of Bengal Florican, this must be done at scale, and quickly.

The population of Bengal Florican in India is estimated at 147–198 adult territorial males (or 350–400 individuals assuming an equal sex ratio) and the total population in Nepal is thought to be fewer than 100 individuals (Collar et al. 2017). In Cambodia, although there is significant inter-annual variation in population estimates within sites
(Figure 4), population size and trends of Bengal Florican are well understood owing to intensive long-term monitoring using a standardized methodology that minimizes the potential for double-counting of males. In contrast, populations in India and Nepal are monitored less frequently and utilize a number of different methods, for instance, in Nepal some sites are surveyed using “sweep counts” that aim to flush birds in a similar way to the non-breeding season census we conducted in Cambodia, whilst at other sites and in India displaying males are located and territories mapped accordingly (Rahmani et al. 2016a; Rahmani et al. 2016b; Jha et al. 2018). Although in some circumstances these methods are more likely to give accurate population estimates, they are also more likely to double-count males and, because they are not standardized, trends are harder to assess. It is possible that populations in some sites in India and Nepal may be over-estimated and declines might be obscured until they are severe. Safety considerations specifically related to the presence of Tiger *Panthera tigris*, Asian Elephant *Elephas maximus* and Indian Rhinoceros *Rhinoceros unicornis*, preclude monitoring on foot following exactly the same method used in Cambodia. Habitats also differ from Cambodia. The sites where Bengal Florican occurs in India and Nepal are a heterogeneous mix consisting of large areas of floodplain grassland within a matrix of deciduous forest (Rahmani et al. 2016a). Given the declines experienced by all other South and Southeast Asian bustard taxa, we recommend testing a modification of the Cambodian method, in which grasslands are mapped, 1 km² survey squares randomly allocated across grassland and surveyed as in Cambodia (but from observation towers, the roofs of vehicles and elephant-back rather than on foot) and these data used to calculate population estimates (displaying males) as in Cambodia but using area of grassland rather than area of site. In addition, because population estimates for *H. b. bengalensis* assume an equal sex ratio, the
actual population may be considerably lower if sex ratios are similar to those recorded in Cambodia. There is an urgent need to evaluate the sex ratio of Bengal Florican populations in India and Nepal.

The current total population, contraction of range and rate of decline of *H. b. blandini* are similar to, and as concerning as those experienced by the Great Indian Bustard *Ardeotis nigriceps* and Lesser Florican *Sypheotides indicus*. Like Cambodia’s Bengal Florican population, the Great Indian Bustard declined from a few thousand in the 1980’s and 1990’s to 600–700 in around 2000, by 2010 the population was thought to be just 300 individuals spread across eight sites (Dutta et al. 2010). By 2014 the population had declined to 200 individuals (Collar et al. 2015), and in 2017 it was estimated that only 170±63 adults remained in just a fraction of its former range, with most of the population at just one site (Collar et al. 2017). Lesser Florican also underwent a similar, but less well studied, decline during the same period, dropping from 1,103–1,765 males during 1994–1999 to about 270 males in 2017 (Dutta et al. 2018). All three species have been massively impacted by loss of grassland and intensification of agriculture (Collar et al. 2017).

The conservation measures described here represent the last hope for the *blandini* subspecies of Bengal Florican and will have to be pursued vigorously to prevent its extinction within five years. The causes of its catastrophic decline are extremely similar to those that imperil Great Indian Bustard, although collisions with power lines have played a more important role in the decline of that species (Collar et al. 2015), at least until now (Mahood et al. 2016). There may also be similarities to the
factors threatening the poorly known Lesser Florican, which is also largely restricted to farmland outside of protected areas. Bengal Floricans in India and Nepal breed almost entirely in protected areas but spend the non-breeding season in farmland, so they may face similar threats (Jha et al. 2018). Successful community-based conservation models implemented at Stoung-Chikraeng BFCA could possibly be modified and applied in India and Nepal to reduce the chance of extinction of those bustard taxa. Collaboration between bustard conservationists in Asia is essential to refine monitoring methods, reduce duplication of research and rapidly apply conservation lessons. Whilst losing just one of these bustard taxa would be a tragedy, failing to work together increases the risk of extinction for all. Preventing the extinction of these charismatic bustards is one of the greatest priorities, and biggest challenges, facing conservation in Asia.

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Chapter 4.

A systematic expert-based assessment of progress and priorities for conservation of the Bengal Florican *Houbaropsis bengalensis*

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Article impact statement

Conservation management can be improved by systematically evaluating successes and priorities, and planning collaboration between organisations.

Running head

Systematic planning of collaboration

Key words

Measuring conservation progress, Species working groups, Systematic threat assessment, Preventing extinction

Abstract

We used six recently developed metrics to measure progress in conservation of the Bengal Florican (*Houbaropsis bengalensis*) and identify priorities for action. The metrics, namely: 1) current threat impact, 2) research need, 3) research achievement, 4) management need, 5) management achievement, and 6) percentage threat reduction, were calculated using information derived from expert elicitation. Using the metrics we identified four priority threats, namely predation by dogs, hunting, power lines and vegetation changes caused by human activities. Although there has been little progress in addressing predation and power lines, we note that reductions in hunting have been achieved and that practitioners have a good understanding of how to ameliorate vegetation changes. We assessed conservation needs across all sites that support Bengal Florican, and highlight conservation achievements at Stoung-Chikreang Bengal Florican Conservation Area (BFCA), Manas National Park and Kaziranga National Park. Using the metrics we developed a framework for
prioritizing collaboration on tackling priority threats, although note that the metrics cannot assess threat impacts where knowledge of sites is limited, such as in much of the non-breeding habitat. Based on existing knowledge, we highlight D’Ering Wildlife Sanctuary in India as one of the highest priority sites for Bengal Florican conservation, and propose that conservation in Stoung-Chikreang Bengal Florican Conservation Area (BFCA), Manas National Park and Kaziranga National Park must be continued, scaled-up and replicated at Baray BFCA and Koshi Tappu Wildlife Reserve. If these plans are followed, then we believe that priority threats can be adequately addressed and the extinction of Bengal Florican can be prevented.

**Introduction**

Bustards are one of the most threatened groups of birds, and the situation in Asia is particularly acute (Collar et al. 2017). Of the six species recorded in the region, all are considered globally threatened or Near Threatened, of these, two are Critically Endangered and one Endangered (BirdLife International 2018). Asia’s bustards face four main threats: habitat loss, degradation and disturbance; power line impacts; hunting and poaching; and anthropogenically enhanced levels of predation (Collar et al. 2017). These threats are familiar by-products of rapid human population growth and economic development, and are common to most threatened species (Maxwell et al. 2016).

Of the two Critically Endangered Asian bustards, the Bengal Florican *Houbaropsis bengalensis* is polytypic with *H. b. bengalensis* confined as a breeding bird to protected areas in floodplain and alluvial grasslands in north and north-east India and
southern Nepal, and H. b. blandini now restricted to the Tonle Sap floodplain of Cambodia (Collar et al. 2018; Mahood et al. 2019). The population is highly fragmented and, during the breeding season, it is largely confined to protected areas. Bengal Floricans migrate from protected areas to unprotected agricultural or lightly wooded areas during annual flooding of breeding grounds, with some birds spending more than half of the year outside of protected areas (Packman 2011; Jha et al. 2018). A recent status review revealed that the population of H. b. blandini is the smallest of any bustard taxon, and is declining at a rate of > 10% per year (Mahood et al. 2019). The population of H. b. bengalensis is 350–400 adult birds (assuming an equal sex ratio) in India and <100 adult birds in Nepal (Collar et al. 2017), and although recent population trends are not clear overall, local declines have been documented at some protected areas (Jha et al. 2018). Evidently, conservation of the Bengal Florican must address threats at all stages of its life-cycle, through working with government to improve the effectiveness of protected areas and with communities and the private sector to address threats on agricultural land. We, the authors, represent the organisations that are trying to achieve these aims and protect the Bengal Florican. However, because we all work at different sites there is little information-sharing between our organisations, even on basic concepts such as threats, management interventions that have been tried, successes and failures. We formed a species working group because we believe that through sharing lessons learned and pooling expertise, we can increase the chance of survival for the Bengal Florican.

Species working groups are formed to make the best use of available resources and reduce the risk of extinctions (IUCN 2018). The knowledge of people (experts) in the group can be a useful resource to assess and prioritise threats and actions, particularly
when there is little published or easily accessible information (Hockings 2003; Martin et al. 2005). Experts can also provide nuanced opinions or perspectives that cannot be achieved by a non-expert reviewing the literature (Johnson & Gillingham 2004). Here, we suggest how knowledge of members of a species working group can be used to prioritise threats, assess conservation progress and plan for action by using a standardised framework for synthesizing expert opinion on threats to taxa, using the Bengal Florican as an example. To do so we adopted and modified methods that have been used to assess the relative importance of different threats to Australia’s globally threatened bird taxa and measure progress towards researching and addressing those threats (Garnett et al. 2018). As well as quantifying the impacts of threats and the need for action, the framework also aims to quantify progress in ameliorating threats. Using the framework, we generated six metrics that describe current threat impact, research and management need, research and management achievement and percentage threat reduction for each threat facing Bengal Florican and for each management unit where it is found (Appendix S1). We use these metrics to plan collaboration systematically, by identifying priority conservation needs and sites where there is already experience in ameliorating those threats. We show how this approach can be used to: 1) systematically assess threats; 2) assess progress in addressing those threats; 3) prioritise conservation actions; and 4) identify potential areas for collaboration among organisations.

**Methods**

We treated the extant populations of breeding Bengal Florican as 14 independent management units (10 for *H. b. bengalensis* and 4 for *H. b. blandini*: Fig. 1, Appendix
S1) based on geographic discreetness, management regime and political boundaries. Birds are likely to move between some of these management units. In South Asia these management units are discrete protected areas (7), groups of geographically proximate protected areas (1: Uttar Pradesh), or unprotected areas that support Bengal Floricans (namely Koklabari Rice Farm, which is legally part of Manas National Park (NP) but managed completely differently; and islands along the Brahmaputra River in Assam, hereafter *chaporis*). In Cambodia the management units were defined in 2005 and have been used by Wildlife Conservation Society (WCS) for research and conservation ever since (Gray et al. 2009; Packman et al. 2013). Although all management units are centered on Bengal Florican breeding grounds, the threat assessment also attempted to include threats acting on birds in the known or assumed non-breeding grounds that correspond to each management unit. Bengal Floricans are faithful to breeding sites (Packman 2011; Jha et al. 2018), and although birds from different management units mix during the non-breeding season they return to the same territories each year during the breeding season.

Figure 1. Locations of the management units used in the assessment. Note:

Management units named as follows: South Asia: (SH) Shuklaphanta NP, (CW) Chitwan NP, (KS) Koshi Tappu WR, (UP) Uttar Pradesh, (MA) Manas NP, (KO)
Assessments were conducted using a semi-structured process as follows. First, a workshop was convened on 26 April 2017 in Phnom Penh, Cambodia, at the end of a study tour around Bengal Florican sites attended by fourteen staff or government counterparts from five NGOs that work on Bengal Florican conservation (Aaranyak, Bombay Natural History Society and The Corbett Foundation from India, Wildlife Conservation Society (representing Cambodia), and Bird Conservation Nepal). All of the non-government organizations of direct relevance to Bengal Florican conservation were represented, and all participants are co-authors on this paper. The participants were provided with an overview of the method and training on the meaning of the terms used. For each management unit, the participants with the most knowledge of the site(s) worked together to (i) identify the threats affecting Bengal Florican at the site(s) from a list of all IUCN threats, (ii) assess the timing, severity and impact of each threat to the Bengal Florican management unit under the current management regime, (iii) assign the level of understanding about how to manage each threat (Management Understanding), and success in managing it at the site(s) (Management Implementation). Threats were categorized using the IUCN Red List threat classification scheme down to Level 3 where possible (Appendix S2) (IUCN 2012a). Participants assessed timing (ongoing, may occur or return in the short term, may occur or return in the distant future), scope (the proportion of the site affected by the threat) and severity (the rate of population decline caused by the threat at the site), following (IUCN 2012b). All responses were checked by the primary author,
uncertainties validated through follow-up conversation with the participants and email discussion, and results shared by email to enable participants to comment and modify responses as needed. This information was then augmented with responses to follow-up questions targeting additional individuals from the Bombay Natural History Society who could not attend the workshop. We did not attempt to quantify anchoring or over-confidence in estimates to reduce biases, but used weighting (see below) to give greater importance to threats and/or conservation interventions that have a greater impact. Costs of conservation interventions were not included in our assessment because a. in many cases it was difficult to disaggregate Bengal Florican specific conservation interventions from general protected area management activities that would have incidentally benefitted Bengal Florican, and, b. relative cost of activities differ between the countries in the assessment, making comparison difficult.

Metrics, summarised in Table 1, were calculated as follows. First, following (Garnett et al. 2018), a weighted threat impact score (IUCN 2012b) was calculated for each threat (t) for each management unit (x), both under current management and under a counterfactual scenario (Ferraro & Pattanayak 2006) that assumed no conservation management of the threat had been undertaken since 1990. For each management unit we then assessed the extent of knowledge of how to manage each threat (MU_t) on a scale of 0 and 6, and the extent to which that knowledge is being applied (MI_t), also on a scale of 0 and 6 (See Table 2 of (Garnett et al. 2018); Appendix S1). For each threat we then calculated weighted levels of need and achievement in research and management and percent threat reduction, again following methods in (Garnett et al. 2018). However, whereas (Garnett et al. 2018) calculated these metrics for each threatened Australian bird taxon, we calculated them for each Bengal Florican.
management unit. The other difference to (Garnett et al. 2018) was that we weighted
the measures of Research Need $RN_t$ and Management Need $MN_t$ by the number of
displaying males within the relevant management unit $N_x$. Weighting conservation
needs in this way gives greater importance to threats that impact more Bengal
Floricans. To this end formulae within (Garnett et al. 2018) were modified such that:

$$RN_{xt} = I_{xtc} \times \left(1 - \frac{(MU_{xt} \times N_x)}{(MU_{\text{max}} \times N_x)}\right) \quad (1)$$

$$MN_{xt} = I_{xtc} \times \left(1 - \frac{(MI_{xt} \times N_x)}{(MI_{\text{max}} \times N_x)}\right) \quad (2)$$

Where $MU_{xt}$ and $MI_{xt}$ are management understanding and implementation
respectively for each threat $t$ on Bengal Floricans in management unit $x$, $MU_{\text{max}}$ and
$MI_{\text{max}}$ are both 6, $I_{xtc}$ is the impact of threat $t$ on Bengal Floricans in management
unit $x$ under the assumption that there has been no management and $N_x$ is the
population of Bengal Floricans in management unit $x$ (See Table 1 and 2 of (Garnett
et al. 2018)). We did not weight the metrics for Research Achievement, Management
Achievement and Percent Threat Reduction by population size because we wanted to
identify management units where conservation had been successful regardless of the
size of the population.

The metrics above were used to develop a framework to guide potential collaboration
in research ($CR_{xt}$) and management ($CM_{xt}$) of priority threats. This was done by
identifying management units with similar threats, and then for each threat, matching
management units where there had been success at alleviating that threat (high
Research or Management Achievement scores) with management units with low 
Research or Management Achievement scores. It is not financially or logistically 
practical to address all threats acting on every subpopulation, so for each 
subpopulation we prioritized threats based on Management Need scores and truncated 
the list of threats when the cumulative score reached 50% (where multiple threats had 
identical scores and the 50% cut off fell within this group, we retained all of those 
threats in our final list). Total Research Achievement ($RA_{xt}$) and Management 
Achievement ($MA_{xt}$) scores were used to prioritize subpopulations to assist in 
alleviating threats. Potential for collaboration on addressing each of the priority 
threats through research ($CR_{xt}$) and management ($CM_{xt}$) were then calculated such 
that:

$$CR_{xt} = RN_{xt} \times RA_{xt} \quad (3)$$

$$CM_{xt} = MN_{xt} \times MA_{xt} \quad (4)$$

Where RN and RA are research need and research achievement scores for each threat 
t at each site $x$, and MN and MA are management need and management achievement 
scores for each threat $t$ at each site $x$. The list of subpopulations to assist in alleviating 
threats was truncated by removing those subpopulations that made no additional 
contribution to threat alleviation. High $CR_{xt}$ or $CM_{xt}$ scores for a given pair of sites 
indicate that there would be significant benefit from collaboration in research or 
management of threats respectively.
Table 1. Summary of metrics used to characterize threat, conservation progress and conservation needs for Bengal Florican, following Garnett et al. in press, for which see for formulae and detailed methods.

<table>
<thead>
<tr>
<th>Metric</th>
<th>What the metric measures</th>
<th>Summary of how the metric is created</th>
</tr>
</thead>
<tbody>
<tr>
<td>Current threat impact</td>
<td>The total population decline over ten years or 3 generations (whichever longer) likely to be caused by a given threat (i.e., the product of scope and severity) at a given site, weighted by threat timing.</td>
<td>Experts assess the timing, scope, and severity of each threat to create weighted threat impact scores (for weightings see Garnett et al. in press).</td>
</tr>
<tr>
<td>Research achievement</td>
<td>The level of understanding about how to manage each threat at each site, or all of the threats acting on a site.</td>
<td>Weighted indicators of progress in research and management are used to characterise need or achievement for each threat acting on each population and create research and management understanding and implementation scores. For each threat at each management unit, management understanding or implementation scores are divided by the maximum management understanding or implementation scores and multiplied by threat impact scores to create research or management threat impact scores.</td>
</tr>
<tr>
<td>Management achievement</td>
<td>The level of success in managing each threat at each site, or all of the threats acting on a site.</td>
<td></td>
</tr>
<tr>
<td>Research need</td>
<td>The deficiency in understanding about how to manage each threat at each site, or all of the threats acting on a site.</td>
<td>For each threat at each management unit, threat impact scores are multiplied by management understanding or implementation score and divided by the maximum management understanding or implementation score to create research or management achievement scores.</td>
</tr>
<tr>
<td>Management need</td>
<td>The deficiency in experience in managing each threat at each site, or all of the threats acting on a site.</td>
<td></td>
</tr>
<tr>
<td>Percent threat reduction</td>
<td>Reduction in threat impact as a result of research and management achievement.</td>
<td>The percent difference between the estimated rate of decline from a threat and the rate that could be occurring had there been no management.</td>
</tr>
</tbody>
</table>


Results

Overall patterns

Across the 14 management units we identified 45 different threats (Appendix S2). Individual management units faced a mean of 16 threats (range: 9-29). *H. b.* *bengalensis* faced a total of 40 different threats (mean: 16, range: 9-29 per management unit), whilst we identified only 18 threats (mean: 16, range: 12-18 per management unit) to *H. b. blandini*. Both taxa faced threats across the same 11 IUCN Level 1 threat categories.

Variation between taxa

When results from all management units were combined, predation by dogs ranked as the most significant threat to Bengal Florican, although it was more important in Cambodia than in South Asia (Fig. 2a and 2b). Otherwise the higher-impact threats differed between the two Bengal Florican taxa. *H. b. bengalensis* was judged to be most at risk from vegetation changes caused by increased fire frequency, invasive plants and changing fluvial processes. Power lines, hunting and to a lesser extent agricultural changes, were identified as the key threats to *H. b. blandini*.

Conservation achievements also differed between the taxa. The greatest reduction in threat to *H. b. bengalensis* has been achieved through reducing encroachment onto protected areas by people building homes and practicing small-scale rice cultivation,
grazing cattle and cutting grass (Fig. 2c). In Cambodia, a reduction in threat from hunting and intensive rice cultivation has only been achieved at Stoung-Chikreang Bengal Florican Conservation Area (BFCA) (Fig. 2d). Research and Management Achievement scores demonstrate that there is a paucity of information and best practice available to deal with most threats to any one taxon (Fig. 2e–h). In general, the metrics indicate that there is a better understanding of threats in Cambodia, but more examples of good management in India and Nepal. There are some specific examples where participants felt that there was a good understanding of how to address threats (such as small-scale rice cultivation and hunting), and that this understanding could be backed up by working examples of good management that could be followed elsewhere. Some threats, such as mitigating the impact of large-scale rice cultivation, were well understood for one taxon, but not for the other, whilst others such as power lines were well understood, but lacked examples of effective mitigation.

There was little overlap in priority Research and Management Needs between the taxa, although predation by free-ranging and domestic dogs must be addressed in all countries (Fig. 2i–l). For *H. b. blandini* the priorities are to mitigate the impacts of power lines, to reduce hunting and stop the spread of agro-industrial agriculture onto the floricans’ remaining habitat. There are more priority Research and Management Needs for *H. b. bengalensis*, which encompass addressing the impacts of changing fluvial processes and increased fire frequency, together with invasive plants and associated vegetation changes. Mitigating small-holder activities such as grass cutting and cattle grazing in some protected areas during the breeding season, and potentially
across the non-breeding range (especially intensification of agriculture), also remain a priority in India and Nepal.
**Figure 2.** Normalized scores for threats summed across all management units that support Bengal Florican for six metrics. 2a and 2b. threat impact weighted by number of displaying males in each management unit for *H. b. bengalensis* and *H. b. blandini* respectively, 2c and 2d. percent threat reduction weighted by number of displaying males in each management unit for *H. b. bengalensis* and *H. b. blandini* respectively, 2e and 2f. naïve research achievement for *H. b. bengalensis* and *H. b. blandini* respectively, 2g and 2h. naïve management achievement for *H. b. bengalensis* and *H. b. blandini* respectively, 2i and 2j. research need weighted by number of displaying males in each management unit for *H. b. bengalensis* and *H. b. blandini* respectively, and, 2k and 2l. management need weighted by number of displaying males in each management unit for *H. b. bengalensis* and *H. b. blandini* respectively.

**Variation between management units**

The metrics indicate that the impact of threats varied substantially between management units (Fig. 2a). Threat impact was scored very high at Shuklaphanta NP in Nepal, Kaziranga NP in India and Baray BFCA and Sankor in Cambodia. The metrics indicate that threats to the unprotected Brahmaputra *chaporis* and Chitwan NP have had few known impacts, although this may be due to a lack of knowledge of site-level threats. No management units have experienced a threat reduction of much more than 50% (Fig. 2b). In Cambodia the only management unit to have achieved more than a negligible reduction in threat level has been Stoung-Chikreang BFCA. In contrast, most of the protected areas in India and Nepal have achieved at least a moderate reduction in the level of threat to Bengal Florican.
Threats have been well researched at most of the management units, and the metrics indicate that Research Achievement has typically led to Management Achievement (Fig. 3c and 3d, Appendix S3). The greatest gains in research and particularly management have been made in Manas NP and Stoung-Chikreang BFCA. Some of the most important sites for Bengal Florican conservation, including D’Ering Wildlife Sanctuary (WS) and the Brahmaputra chaporis in India, Shuklaphanta NP in Nepal and Baray BFCA and Sankor in Cambodia, achieved low scores for Research and Management Achievement. Scores for Research and Management Need scores were highly correlated (Fig. 3e and 3f, Appendix S3). Four sites scored particularly highly, D’Ering WS in India, Koshi Tappu Wildlife Reserve (WR) in Nepal, and Stoung-Chikreang BFCA and Baray BFCA in Cambodia. These management units all have relatively high Bengal Florican populations and are in urgent need of additional conservation actions to ameliorate threats.
Figure 3. Normalized scores for six metrics used to measure conservation progress at all management units that support Bengal Florican. 3a. threat impact, 3b. percent threat reduction, 3c. research achievement, and, 3d. management achievement, are naïve scores; 3e. research need, and, 3f. management need, are weighted by number of displaying males. Note: grey bars are sites that support H. b. bengalensis, white bars are sites that support H. b. blandini; sites are listed from largest (most displaying male Bengal Floricans) to smallest.

The framework for potential collaboration (Table 2) indicates that some of the priority threats at some of the most important sites, such as Koshi Tappu Wildlife Reserve
(WR) in Nepal, and Baray BFCA and Sankor in Cambodia, can be mitigated by drawing on lessons learned at other sites. In particular, there is considerable experience in managing the impacts of small and large scale rice cultivation at Stoung-Chikreang BFCA that could be applied other sites. Shuklaphanta NP has a daunting number of priority threats, but there is research or management experience relevant to most of them at other sites. In contrast, priority threats at D’Ering WS are, in general, poorly known, although we identified opportunities for applying lessons in fire management from Manas NP and Kaziranga NP.
Table 2. Framework for potential collaboration in research (CRxt) and management (CMxt) to ameliorate priority threats. *Note: in this matrix, for each site in the first column, threats are listed in order of management need score such that threats that are a higher priority for management appear higher in the list. To ensure that only high-priority threats are listed, threats for each site are listed until the cumulative Management Need score reaches 50% of the total management need score for the site. Subsequent columns are headed by sites listed in order of their total research or management achievement scores, (site names are abbreviated as follows: Ma: Manas NP, St: Stoung-Chikreang BFCA, Ka: Kaziranga NP, Ch: Chitwan NP, Ko: Koklabari, and, Ks: Koshi Tappu WR). Only sites with high research or management achievement scores are included; darkness of shading indicates the level of potential for collaboration in research or management between a pair of sites to ameliorate a specific priority threat, i.e. darker shading indicates that a priority threat with a high management need at the site in column 1, could be ameliorated by lessons learned about research or management undertaken at sites at the head of the column with the shaded cell.*

<table>
<thead>
<tr>
<th>Sites and priority threats</th>
<th>Research</th>
<th>Management</th>
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<tbody>
<tr>
<td>D’Ering WS</td>
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<td>Increased fire frequency</td>
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<td>Flooding</td>
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<td>Warming climate</td>
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<td>Baray BFCA</td>
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<td>Power lines</td>
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<tr>
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*Chitwan NP*

Habitat shifts

Vegetation changes

**Discussion**

We identified twice as many threats for *H. b. bengalensis* than *H. b. blandini*. Mean threat impact score for *H. b. bengalensis* was 3.9, compared to 3.6 for *H. b. blandini*.

At Stoung-Chikreang BFCA and a number of locations in South Asia threats have been much reduced. However, all Bengal Florican subpopulations are now small, surrounded by human-dominated land-uses and vulnerable to local extinction. With the exception of Stoung-Chikreang BFCA, all of those in Cambodia are declining, whilst population trends in India and Nepal are unclear (Collar et al. 2017). We found substantial variation in the relative importance of threats between the two Bengal Florican taxa. In Cambodia, priority threats are a mixture of modern threats associated with development, such as power lines and large-scale rice cultivation, and threats associated with the traditional lifestyles of the rural poor, particularly hunting and predation by free-ranging dogs. *H. b. bengalensis* breeds almost entirely in protected areas, and the priority threats that we identified mostly relate to the details of protected area management. We identified some sites where participants perceived that progress had been made in ameliorating some threats. We are not able to validate
these reductions in threat through robust experimental evidence, but point to the fact that Bengal Florican is extinct or almost so outside of protected areas as evidence that some conservation progress has been achieved.

The metrics are designed for known threats so cannot provide direction where populations are so little known that threats have not been identified. Undertaking the exercise to populate the metrics, however, highlights areas of ignorance so that knowledge gaps can be identified. Because they are so poorly known, the Brahmaputra chaporis did not rank as a high priority site for conservation intervention even though they are unprotected and support one of the largest sub-populations of H. b. bengalensis (Rahmani et al. 2016a). Bengal Floricans have persisted up until now in relatively large numbers at this site, so there may genuinely be few significant threats there, although this needs to be substantiated by additional research. Threats during the non-breeding season may also have been overlooked, particularly in South Asia where satellite telemetry has only recently begun to reveal where birds spend the non-breeding season (Jha et al. 2018). As the metrics cannot capture the need for action to address threats that have not been identified, we here use the peer-reviewed literature to substantiate the threats that we identified as priorities.

Dogs

In our assessment, predation of adults, chicks and eggs by free-ranging domestic or feral dogs ranked as the highest priority threat in Cambodia, and among the highest in India and Nepal. In Cambodia this threat ranked higher than power lines because
power lines do not affect all of the sites where Bengal Floricans are found. Domestic dogs have contributed to 11 vertebrate extinctions and are a known or potential threat to at least 188 threatened species, including 78 bird species (Doherty et al. 2017). Conservation issues associated with dogs have been recorded from across the world, although Southeast Asia has the greatest number of reported case studies (Doherty et al. 2017). In birds, predation of adults and nests is the main interaction recorded, followed by disruption of feeding and breeding activities (Hughes & Macdonald 2013). Abundance of dogs is rarely quantified, but in parts of rural India where Great Indian Bustard *Ardeotis nigriceps* has recently been extirpated, the population density of free-ranging dogs is 526–969 dogs per km² (Belsare & Gompper 2013). In protected areas in India and Nepal, dog populations are possibly suppressed due to predation by large wild carnivores, especially Leopards *Panthera pardus*, and some protected areas that support Bengal Floricans are relatively distant from source populations of dogs. This contrasts with the situation in Cambodia where Leopards are extinct in areas where Bengal Floricans occur (Rostro-García et al. 2016), protected areas are located close to human habitation and dogs wander freely through protected areas. Predation of bustards or their nests is rarely confirmed, which is unsurprising because Bengal Floricans are rare and therefore predation is probably an infrequent event, although the remains of a female Bengal Florican and its nest that had been predated by dogs was found in Cambodia (S. Mahood pers. obs.) and an attack on an adult bird was witnessed in India (Home et al. 2018). We may also have underestimated the impact of dogs on *H. b. bengalensis* in the non-breeding season, particularly in South Asia (Jha et al. 2018). Addressing the threat of dogs is a priority for both Bengal Florican taxa, and although there is some experience from Chitwan NP and Koklabari that can be used elsewhere (Table 1), the problems caused by dogs
have not been solved anywhere. Culling is culturally incompatible in much of India and Nepal, and causes tensions between law enforcement agencies, animal rights activists (in India) and local communities. Fencing and neutering may reduce predation in protected areas, but will be impractical or insufficient outside of them. Across the range of Bengal Florican there is a need to work rapidly and simultaneously with law enforcement agencies and communities to find practical solutions to mortality caused by dogs.

**Power lines**

A power transmission line (currently under construction) that will bisect the migration route of almost the entire Cambodian Bengal Florican population ranked second on the list of threats facing *H. b. blandini*. Power lines are a well-documented threat to birds globally (Jenkins et al. 2010), with hundreds of millions of birds killed annually through collisions and electrocution (Rioux et al. 2013; Loss et al. 2014). A review of 23 studies encompassing six bustard taxa found a mean rate of fatalities as a result of collisions with power lines of 0.69 per km per year when power lines were routed through areas supporting concentrations of bustards (Mahood et al. 2016). Collisions with power lines are causing a >50% global decline over thirty years in Ludwig’s Bustard *Neotis ludwigi* (Jenkins et al. 2011). In Cambodia, the new power transmission line is routed through one of the most important leks at Stoung-Chikreang BFCA and has the potential to cause the extinction of this sub-population, as well as declines in most of the other sub-populations (Mahood et al. 2016). The company building the power line agreed to use bird flight deflectors where the line crosses Stoung-Chikreang BFCA, although this is likely to be insufficient to reduce
mortality rates significantly because, unlike storks and cranes, bustards cannot see
bird flight deflectors (Jenkins et al. 2010). In Europe, power lines have occasionally
been buried to prevent bustard mortality (Raab et al. 2012), but this is extremely
costly and is not technologically possible in all situations. Power lines were not
identified as a significant threat for *H. b. bengalensis*. The importance of this threat in
India and Nepal may have been underestimated due to a lack of information,
particularly in non-breeding locations. Even if power lines are not currently a threat to
*H. b. bengalensis*, they are a potential future threat worthy of research. There are
plans for a massive increase in the number and capacity of hydropower dams on rivers
along the lower slopes of the Himalayas (Grumbine & Pandit 2013), and there will be
a need to transport this power to the densely populated lowlands using power lines
that might cross locations inhabited by Bengal Floricans.

_Hunting_

Our assessment ranked reducing hunting as the greatest achievement in Bengal
Florican conservation to date (here hunting refers to the deliberate killing of adults
and the taking of eggs). Hunting is one of the greatest threats facing tropical wildlife
(Milner-Gulland & Bennett 2003), and after invasive species, is the most significant
driver of bird extinctions (Butchart et al. 2018). Threats that cause adult mortality
have the greatest impact on species with high survival and low fecundity rates, such
as bustards (Dolman et al. 2015). Bustards are large-bodied and slow-flying, making
them desirable hunting targets, hunting is a threat to all Asian bustard species, causing
local population declines and extinctions (Collar et al. 2017). Hunting caused the
collapse of the Cambodian population of Bengal Florican during the 1970s and 1980s.
(Goes 2013), and it was also formerly a more significant threat in India and Nepal. Hunting of Bengal Floricans has been reduced through collaboration with law enforcement agencies, better protected area management, and by promoting performance-based nest protection payments among communities (Cambodia only). Despite these conservation gains, hunting is still a major threat to Bengal Florican, particularly outside protected areas where local people still predate nests (Cambodia), or kill any large birds they encounter for food (C. Hong pers. obs.). Our framework for collaboration indicates that there is experience in reducing hunting at a range of sites (Table 2), which should be utilized widely. Better law enforcement is a vital tool to prevent hunting, but advocacy among communities is also essential to build local pride in Bengal Floricans and create peer pressure to stop hunting. These measures need to be supplemented by alternative livelihood schemes with financial benefits linked to conservation outcomes (such as eco-tourism), and measures to ensure that nutritional needs of local people can be met by legal means.

**Habitat change**

Intensification of agriculture is one of the greatest threats to Cambodia’s Bengal Florican population. However, it is possible that our threat assessment underestimated its impact because data suggests that habitat loss alone could account for the decline in Cambodia’s Bengal Florican population (Mahood et al. 2020). Agricultural activity, particularly cropping, is the most prevalent threat facing threatened and near-threatened species worldwide (Maxwell et al. 2016). Conversion of natural habitat to agriculture is disastrous for many bird species (e.g. primary forest dependent species), but the impacts on species are nuanced and some species can tolerate and even thrive
in human-dominated landscapes (Laurance et al. 2014). Extensive, low-intensity farmland is now essential for a range of non-forest species in Europe, but this leaves farmland bird populations vulnerable to changes in agricultural land-use and intensity (Jerrentrup et al. 2017). For example in Europe Little Bustards now rely on cereal pseudo-steppes, with their breeding success so tied to agricultural intensity (Lapiédra et al. 2011) that recent changes in agricultural practices caused population declines (Delgado & Moreira 2010). In Cambodia, Bengal Florican historically bred in deep-water rice fallows, which have a structure similar to grassland (Gray et al. 2007). During the early 2000s, farmers switched from a wet-season rice crop to a single crop of irrigated dry-season rice, eliminating the Bengal Florican’s favored farmland mosaic habitat (Gray et al. 2007; Packman et al. 2013). Although it appears that Bengal Floricans can tolerate cultivation of a single crop of dry-season rice per year in the breeding grounds, the recent shift to two rice crops per year leaves no dry land on which the birds can nest (Ibbett et al. 2019). Agricultural expansion and intensification has been restricted, if not entirely prevented, at Stoung-Chikreang BFCA, and this achievement needs to be replicated at Baray BFCA although financial resources are the main impediment. Different solutions are needed in unprotected areas such as Sankor and in the unprotected areas close to Baray BFCA where Bengal Floricans also remain. Trials are ongoing in the non-breeding areas in Cambodia to develop rice farming methods that are compatible with Bengal Florican conservation, informed by best practice from Europe (Bretagnolle et al. 2011; Morales et al. 2013). If successful these should be rapidly scaled up at Sankor and in the unprotected areas close to Baray BFCA.
In India and Nepal, habitat change caused the extinction of almost all breeding populations of Bengal Florican outside protected areas as a result of unsustainable grass-cutting, small-scale rice cultivation, cattle grazing, and scrub encroachment after flood regimes were altered to facilitate agricultural intensification (Dutta et al. 2013). Agricultural intensification in the non-breeding range of *H. b. bengalensis* is ongoing, and since quality of non-breeding habitat can influence nesting success in migratory birds (Norris et al. 2004), there is a need to promote agricultural techniques that permit bustards to persist in these farmland areas. Inside protected areas, grass-cutting, small-scale rice cultivation and cattle grazing have been reduced by excluding people from protected areas (Baral et al. 2012; Rahmani et al. 2012; Baral et al. 2013). However, habitat change is still the greatest threat to *H. b. bengalensis*, except that now it is caused by inappropriate fire regimes, invasive vegetation and changes in flood regime that promote succession. With the exception of D’ Ering WS, most South Asian protected areas with Bengal Floricans are managed for large, charismatic species such as Indian Rhinoceros *Rhinoceros unicornis*. Grasslands are managed by using fire early in the breeding season of grassland birds to create fodder for large herbivores which, coupled with changes in flood regimes, favors invasive plant species such as *Mimosa diplotricha, Chromolaena odorata* and *Mikania micrantha*, thereby reducing the suitability of grassland for Bengal Florican. These threats have already caused the local extinction of Bengal Floricans from a number of protected areas in Uttar Pradesh and Assam, and are driving declines even in strongholds such as Manas NP (Rahmani et al. 2012; Rahmani et al. 2016a). Trials are underway in several protected areas that aim to test the effectiveness of different methods for removal of invasive plants and scrub, and the vegetational impacts of reducing the frequency or changing the timing of burning. With good communication of outcomes
among Bengal Florican practitioners, these trials could inform management across relevant sites in India and Nepal.

**Geographic priorities for Bengal Florican conservation**

Progress has been made in reducing the impacts of threats at some locations, but there is much work still to be done at some of the largest subpopulations where threat impacts are greatest, such as Sankor and Baray BFCA in Cambodia, Koshi Tappu WR in Nepal, the Brahmaputra *chapors*, Koklbari and D’Ering WS in India. The framework for potential collaboration (Table 1) is a novel attempt to structure collaboration on research and management and prevent duplication of activities. It indicates that most of the priority threats at sites with the largest sub-populations could be addressed at those sites through applying lessons learned in Manas NP, Kaziranga NP and Stoung-Chikreang BFCA. Under this scenario, more than two thirds of the global Bengal Florican population would be under species-specific conservation management. The metrics indicate that D’Ering WS is the most important site in India for Bengal Florican conservation, and additionally it supports some of the largest populations of the passerines that are endemic to floodplain grasslands in South Asia (Rahmani et al. 2016b). Since it is not (yet) managed for large herbivores, it presents a unique opportunity to manage habitat specifically for Bengal Floricans and other grassland-dependent birds. The metrics also underline the importance of continuing, and improving, the ongoing conservation efforts at Stoung-Chikreang BFCA and Koshi Tappu WR, these sites represent the best chance for Bengal Floricans in Cambodia and Nepal respectively. We identified a number of potential areas for collaboration within the Bengal Florican working group. Some
sites with small Bengal Florican populations can also be rescued without the need for novel research. For instance, almost all priority threats at Shuklaphanta NP can be ameliorated to a degree through applying lessons learned in Manas NP, and replicating the achievements of Stoung-Chikreang BFCA is a high priority for Baray BFCA. The framework indicates that there is particularly strong expertise in mitigating the impacts of large and small-scale rice (for instance at Stoung-Chikreang BFCA) and hunting (at a range of sites), expertise can be transferred to sites where this is needed. It also indicates that there are some deficiencies in expertise that cannot be met within the Bengal Florican working group, these are priorities for outside assistance. In addition to the measures discussed above, captive breeding should be considered, although a thorough discussion of the merits of captive breeding is beyond the scope of this paper.

Conclusions

We used a systematic approach to avoid developing a bewildering and unachievable list of conservation priorities. Although we used the same metrics as (Garnett et al. 2018), we used them to assess conservation progress, needs and opportunities across the management units occupied by one species, rather than to compare progress in conservation across a group of taxa. We found that the metrics had significant utility for this purpose, although they were vulnerable to geographic variation in availability of information, which was less apparent in the Australian study. By weighting threat scores by the number of Bengal Floricans in each management unit, our objective prioritisation of action and collaboration is not skewed by threats that are disproportionately important at locations where there are few Bengal Floricans. The
method we used was low-cost, transparent and was not perceived as critical of any one organization. Moreover, it fostered positive relationships that will facilitate ongoing sharing of expertise under the framework for collaboration. Although our metrics are vulnerable to information deficiencies, our results are compatible with the conservation literature and we recommend our approach as a first step for planning collaboration among members of a species working group. The framework for potential collaboration only addresses priority (high scoring) Research and Management Needs, so high Potential Collaboration ($CR_{st}$ and $CM_{st}$) scores can only be achieved if there are sites that have high Research or Management Achievement scores, for our purpose there would be little utility in identifying threats combinations of low Research or Management need and high Research or Management Achievement. The priority threats that we identified are the same as those facing Great Indian Bustard, Lesser Florican *Sypheotides indicus* and other Asian bustard species (Collar et al. 2017). Given the very real risk of extinction facing all of Asia’s bustards, collaboration and information sharing is essential to make the best use of limited time and resources. The long-term persistence of the Bengal Florican and other Asian bustards depends on solving the threats detailed above, sharing information among practitioners and rapidly applying lessons from sites where threats have been reduced.

**Acknowledgements**

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Supporting Information
Management units used in the analyses (Appendix S1), IUCN threats identified in the analysis (Appendix S2), and correlations (R² values) between the five metrics used to measure conservation progress of Bengal Florican (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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**Supporting Information 1.** Management units used in the analyses.

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<td>Dudhwa National Park</td>
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<td>India</td>
<td>1,270</td>
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<td>Manas NP</td>
<td>India</td>
<td>950</td>
<td>12</td>
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<td>Koklabari</td>
<td>India</td>
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<td>20</td>
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<td>Orang National Park</td>
<td>Orang NP</td>
<td>India</td>
<td>79</td>
<td>10</td>
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<td>Kaziranga National Park</td>
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<td>D’Ering WS</td>
<td>India</td>
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<tr>
<td>Laokhowa and Burachaporist Wildlife Sanctuaries</td>
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<td>India</td>
<td>114</td>
<td>7</td>
<td>2013–16</td>
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<td>Majuli area</td>
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<td>6</td>
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<td>2</td>
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<td>India</td>
<td>350</td>
<td>3</td>
<td>2014</td>
<td>2</td>
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<tr>
<td>Amarpur and Sadia area</td>
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<td>India</td>
<td>c.200</td>
<td>19</td>
<td>2016–17</td>
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<td>India</td>
<td>c.100</td>
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<td>6</td>
<td>2014–15</td>
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<tr>
<td>Chitwan National Park</td>
<td>Chitwan NP</td>
<td>Nepal</td>
<td>953</td>
<td>3</td>
<td>2014–15</td>
<td>2</td>
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<tr>
<td>Site</td>
<td>Management Unit</td>
<td>Country</td>
<td>Area (km²)</td>
<td>No. males</td>
<td>Year(s)</td>
<td>Source</td>
</tr>
<tr>
<td>----------------------</td>
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<td>------------</td>
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<tr>
<td>Koshi Tappu WR</td>
<td>Koshi Tappu WR</td>
<td>Nepal</td>
<td>175</td>
<td>31</td>
<td>2017</td>
<td>2</td>
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<tr>
<td><strong>Sub-total</strong></td>
<td></td>
<td></td>
<td></td>
<td><strong>214</strong></td>
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<tr>
<td><strong>TOTAL</strong></td>
<td></td>
<td></td>
<td></td>
<td><strong>353</strong></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Notes:* Sites with no Bengal Floricans in most recent survey were excluded. Sources are: 1 = Mahood *et al.* 2019; 2 = Collar *et al.* 2017 and sources therein.
Supporting Information 2. IUCN threats identified in the analysis

The full list of threats can be found at http://www.iucnredlist.org/technical-documents/classification-schemes/threats-classification-scheme

<table>
<thead>
<tr>
<th>Full IUCN threat name</th>
<th>Short name</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Residential &amp; commercial development</td>
<td></td>
</tr>
<tr>
<td>1.1 Housing &amp; urban areas</td>
<td>Urban development</td>
</tr>
<tr>
<td>1.2 Commercial &amp; industrial areas</td>
<td>Commercial development</td>
</tr>
<tr>
<td>1.3 Tourism &amp; recreation areas</td>
<td>Tourism development</td>
</tr>
<tr>
<td>2. Agriculture &amp; aquaculture</td>
<td></td>
</tr>
<tr>
<td>2.1 Annual &amp; perennial non-timber crops</td>
<td></td>
</tr>
<tr>
<td>2.1.1 Shifting agriculture</td>
<td>Shifting agriculture</td>
</tr>
<tr>
<td>2.1.2 Small-holder farming</td>
<td>Small-holder rice</td>
</tr>
<tr>
<td>2.1.3 Agro-industry farming</td>
<td>Large-scale rice</td>
</tr>
<tr>
<td>2.2 Wood &amp; pulp plantations</td>
<td></td>
</tr>
<tr>
<td>2.2.1 Small-holder plantations</td>
<td>Small-scale plantations</td>
</tr>
<tr>
<td>2.2.2 Agro-industry plantations</td>
<td>Large-scale plantations</td>
</tr>
<tr>
<td>2.3 Livestock farming &amp; ranching</td>
<td></td>
</tr>
<tr>
<td>2.3.1 Nomadic grazing</td>
<td>Nomadic grazing</td>
</tr>
<tr>
<td>2.3.2 Small-holder grazing, ranching or farming</td>
<td>Small-scale grazing</td>
</tr>
<tr>
<td>2.3.3 Agro-industry grazing, ranching or farming</td>
<td>Large-scale grazing</td>
</tr>
<tr>
<td>3. Energy production &amp; mining</td>
<td></td>
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<tr>
<td>3.1 Oil &amp; gas drilling</td>
<td>Oil drilling</td>
</tr>
<tr>
<td>3.2 Mining &amp; quarrying</td>
<td>Mining</td>
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<tr>
<td>4. Transportation &amp; service corridors</td>
<td></td>
</tr>
<tr>
<td>4.1 Roads &amp; railroads</td>
<td>Roads</td>
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<tr>
<td>4.2 Utility &amp; service lines</td>
<td>Power lines</td>
</tr>
<tr>
<td>5. Biological resource use</td>
<td></td>
</tr>
<tr>
<td>5.1 Hunting &amp; collecting terrestrial animals</td>
<td></td>
</tr>
<tr>
<td>5.1.1 Intentional use (species being assessed is the target)</td>
<td>Intentional hunting</td>
</tr>
<tr>
<td>5.1.2 Unintentional effects (species being assessed is not the target)</td>
<td>Non-targeted hunting</td>
</tr>
<tr>
<td>5.2 Gathering terrestrial plants</td>
<td></td>
</tr>
<tr>
<td>Full IUCN threat name</td>
<td>Short name</td>
</tr>
<tr>
<td>------------------------------------------------------------------------------------</td>
<td>----------------------------</td>
</tr>
<tr>
<td>5.2.2 Unintentional effects (species being assessed is not the target)</td>
<td>Grass cutting</td>
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<tr>
<td>5.3 Logging &amp; wood harvesting</td>
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<td>5.3.3 Unintentional effects: subsistence/small scale (species being assessed is not the target)</td>
<td>Forest degradation</td>
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<tr>
<td>5.4 Fishing &amp; harvesting aquatic resources</td>
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<tr>
<td>5.4.3 Unintentional effects: subsistence/small scale (species being assessed is not the target)</td>
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<tr>
<td>6. Human intrusions &amp; disturbance</td>
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<td>6.1 Recreational activities</td>
<td>Tourist disturbance</td>
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<tr>
<td>6.2 War, civil unrest &amp; military exercises</td>
<td>Military disturbance</td>
</tr>
<tr>
<td>6.3 Work &amp; other activities</td>
<td>Other disturbance</td>
</tr>
<tr>
<td>7. Natural system modifications</td>
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</tr>
<tr>
<td>7.1 Fire &amp; fire suppression</td>
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</tr>
<tr>
<td>7.1.1 Increase in fire frequency/intensity</td>
<td>Increased fire frequency</td>
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<tr>
<td>7.1.3 Trend Unknown/Unrecorded</td>
<td>Change in fire frequency</td>
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<tr>
<td>7.2 Dams &amp; water management/use</td>
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<td>7.2.3 Abstraction of surface water (agricultural use)</td>
<td>Water management</td>
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<tr>
<td>7.2.9 Small dams</td>
<td>Irrigation infrastructure</td>
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<tr>
<td>7.2.10 Large dams</td>
<td>Hydropower dams</td>
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<tr>
<td>7.3 Other ecosystem modifications</td>
<td>Other ecosystem modifications</td>
</tr>
<tr>
<td>8. Invasive &amp; other problematic species, genes &amp; diseases</td>
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</tr>
<tr>
<td>8.1 Invasive non-native/alien species/diseases</td>
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<tr>
<td>8.1.1 Unspecified species</td>
<td>Invasive plants</td>
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<tr>
<td>8.1.2 Named species</td>
<td>Predation by dogs</td>
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<tr>
<td>8.2 Problematic native species/diseases</td>
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<tr>
<td>8.2.2 Named species</td>
<td>Vegetation changes</td>
</tr>
<tr>
<td>9. Pollution</td>
<td></td>
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<tr>
<td>9.1 Domestic &amp; urban waste water</td>
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</tr>
<tr>
<td>9.1.1 Sewage</td>
<td>Sewage</td>
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<td>9.3 Agricultural &amp; forestry effluents</td>
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<tr>
<td>9.3.1 Nutrient loads</td>
<td>Agricultural run-off</td>
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<td>9.3.2 Soil erosion, sedimentation</td>
<td>Soil erosion</td>
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<td>9.3.3 Herbicides and pesticides</td>
<td>Pesticides</td>
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<td>Full IUCN threat name</td>
<td>Short name</td>
</tr>
<tr>
<td>--------------------------------------</td>
<td>---------------------</td>
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<tr>
<td>9.4 Garbage &amp; solid waste</td>
<td>Rubbish</td>
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<tr>
<td>11. Climate change &amp; severe weather</td>
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<tr>
<td>11.1 Habitat shifting &amp; alteration</td>
<td>Habitat shifts</td>
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<tr>
<td>11.2 Droughts</td>
<td>Drought</td>
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<tr>
<td>11.3 Temperature extremes</td>
<td>Warming climate</td>
</tr>
<tr>
<td>11.4 Storms &amp; flooding</td>
<td>Flooding</td>
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Supporting Information 3. Correlations ($R^2$ values) between the six metrics used to measure conservation needs and progress of Bengal Florican

<table>
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<tr>
<th></th>
<th>Threat Intensity</th>
<th>Research Need</th>
<th>Management Need</th>
<th>Research Achievement</th>
<th>Management Achievement</th>
<th>Percent Threat Reduction</th>
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<tbody>
<tr>
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<td>0.690</td>
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<td>x</td>
<td>0.865</td>
<td>0.005</td>
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<td>0.011</td>
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<td>Management Need</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>0.052</td>
<td>0.009</td>
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<tr>
<td>Research Achievement</td>
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<td>x</td>
<td>x</td>
<td>x</td>
<td>0.364</td>
<td>0.089</td>
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<tr>
<td>Management Achievement</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>0.164</td>
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<td>Percent Threat Reduction</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>
Chapter 5.

Agricultural intensification is causing rapid habitat change in the Tonle Sap Floodplain, Cambodia

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Abstract

The Tonle Sap Lake and Floodplain (TSLF) supports many globally threatened species and its fishery has sustained Cambodia’s people for millennia. The rate of habitat loss has accelerated in recent years due to political and economic conditions, and a warming climate and El Niño events that created opportunities for people to burn scrubland at an elevated rate. Here, we use a point-based landcover assessment method to document the impacts of local-scale drivers, in particular agricultural intensification, on changes in landcover between 1993 and 2018. The areal extent of scrubland and grassland in the TSLF declined from ~74% in 1993 to ~52% in 2018, as a result of agricultural intensification and expansion, facilitated by intense fires in recent years. During that time period, grassland cover declined from ~3,160 km² to ~519 km², whilst between 2008 and 2018, scrubland cover declined from ~8,660 km² to ~6,776 km². Habitat loss has had catastrophic implications for grassland-dependant species, such as Bengal Florican, and, we estimate that habitat changes in the TSLF may have caused carbon stocks to decline by 12% while fish productivity may have declined by > 6% with significant implications for food security. To put the habitat loss in context, losses over the past ten years have been nearly twice as large as published predictions of the amount likely to be lost between 2010 and 2040 due to hydropower. We suggest that the impacts of agricultural intensification deserve greater attention from policy makers and the development community, because habitat change in the TSLF is a current crisis not just a future problem.

Keywords

Grassland loss, Freshwater fishery, Habitat conservation, Food security, Carbon stock.
Introduction

One of the most biologically diverse and heavily populated ecosystems in the Mekong River Basin is the Tonle Sap Lake and Floodplain (TSLF), which culturally, nutritionally and ecologically defines Cambodia (Campbell et al. 2009). Hydropower on the Mekong River Basin and climate change are considered the main threats to the TSLF (Pokhrel et al. 2018). Their potential future impacts on hydrology, habitats, fish and biodiversity have been extensively researched and are well understood by policy makers (Johnston & Smakhtin 2014; Hecht et al. 2019). However, the immediate impacts of local changes within the TSLF, such as agricultural intensification, have been largely ignored and are not incorporated into policy discussions (Arias et al. 2019).

Connected to the Mekong River by the Tonle Sap River, the TSLF is the largest freshwater lake in Southeast Asia and the world’s largest flood-pulse ecosystem. The flood pulse drives one of the most productive inland fisheries in the world (FAO 2011), with an incredible biomass of local fish and other aquatic organisms augmented annually by vast numbers of juvenile fish of c.300 migratory species that use seasonally flooded habitats such as forest, scrubland and grassland as a nursery ground (Baran 2005). More than 60% of Cambodia’s freshwater fish catch is from the TSLF (Baran 2005), which also supports the world’s largest watersnake harvest (Brooks et al. 2007). Fish make up c.70% of animal protein consumed in Cambodia (higher in the TSLF), constituting c.63 kg/person/year, of which approximately 80% (450,000 tons) is wild-caught freshwater fish (Baran et al. 2014; WorldFish 2014). At
least 1.5 million people live in the TSLF, and reliance on freshwater fish and other aquatic organisms is especially high among the rural poor, including small-scale rice farmers and the >100,000 people who live in floating houses and rely on fishing as their only source of income (Keskinen 2006; Johnston et al. 2013).

Although most modern sources treat the vegetational distribution of the 1990’s as the ‘natural’ state against which predictions of future change should be made (Arias et al. 2012; Arias et al. 2014), the TSLF has long supported a rich ethno-cultural landscape, with farming regimes linked to the annual cycle of the flood pulse (Bonheur & Lane 2002). At least 2,000 traditional rice varieties were cultivated, each adapted to different parts of the floodplain (Home 1997) with deep-water rice planted on the inner floodplain as floodwaters rose and harvested when the water receded (Gray et al. 2007). The fallow deep-water rice fields, together with uncultivated grasslands that were maintained in the inner floodplain by a combination of grazing by domestic cattle and periodic burning, constituted the largest remaining floodplain grassland in Southeast Asia (Bonheur & Lane 2002; Packman et al. 2013a; Parolin et al. 2016) and supported numerous mammal, reptile, fish and waterbird species (Campbell et al. 2006). This cultural landscape has then been greatly altered during the course of the twentieth century with many species now threatened including the Critically Endangered Bengal Florican Houbaropsis bengalensis (Gray et al. 2009; Packman et al. 2013b; Mahood et al. 2019). First, extensive gallery forests were almost entirely destroyed by the French colonial Service Forestier which harvested seven million m^3 of wood from between 1932 and 1945 for fuelwood and charcoal, targeting large trees that are now extremely rare (Ashwell 2017). Then, most important deep-water rice
varieties were lost during the Khmer Rouge regime (1975–1978) and subsequent period of political instability (Home 1997). Some farmers did manage to continue growing some deep-water rice until the early 1990’s (Gray et al. 2007).

The importance of the TSLF for biodiversity and people led to its recognition as Cambodia’s first UNESCO Biosphere Reserve in 1997 (Fig. 1) (UNESCO 2019). The Biosphere Reserve is managed by Ministry of Environment, which has designated three small core zones and larger buffer and transition zones as national protected areas (IUCN category IV and VI respectively). Overlapping with the Biosphere Reserve are 175 Community Fisheries, in which management is devolved to communities, and 58 Fish Sanctuaries, in which fish and seasonally inundated habitats are legally protected, both fisheries and sanctuaries are managed by the Fisheries Administration under the Ministry of Agriculture, Forestry and Fisheries, which also has authority for law enforcement in the flooded forest domain. Part of the Northern Tonle Sap Protected Landscape (NTSPL), which was established to protect habitat used by Bengal Florican, overlaps with the Fish Sanctuaries and buffer zone of the Biosphere Reserve. The NTSPL is managed by Ministry of Environment. The Tonle Sap Authority (TSA) was established under the Cambodia National Mekong Committee, chaired by the Ministry of Water Resources and Meteorology, with a mandate to coordinate management of the TSLF. The TSA created three concentric zones in the floodplain surrounding the lake (known as Zones, 1, 2 and 3), with a greater degree of habitat protection closer to the dry-season limit of the lake.
In planning for changes that will be wrought by hydropower and climate change, consideration must be given to agricultural intensification and the ways in which people in the TSLF might try to adapt to changing ecological conditions caused by climate change and hydropower dams. Here, we respond to recent calls to redress the balance (Uk et al. 2018; Arias et al. 2019). First, we quantify the impact of local human activities, including agricultural intensification, on natural habitats in the TSLF from 1993–2018, compare them with the published results of models predicting the impacts of hydropower and climate change, and estimate how the different types
of landscape transformation have already impacted food security, carbon storage and threatened species. Next, we highlight recent changes in anthropogenic fire in the TSLF and use these to make predictions about how the impacts of climate change and hydropower will interact with agricultural intensification to alter habitats in the TSLF. Finally, we suggest adaptation and mitigation strategies that account for local human activities, contribute to mitigation and adaptation to the impacts of hydropower and climate change, and provide benefits for communities and protect the rich biodiversity of the TSLF.

Methods

Study site

The TSLF is located in the centre of Cambodia (Fig. 1). During the dry season (November-May), the 2,600 km² TSLF has a maximum depth of only about 1.5 m and discharges to the Mekong River via the Tonle Sap River. During the wet season (June to October) the area of open water can exceed 15,000 km² with a maximum depth of over 10 m. The extent and duration of the flood varies annually (Kummu & Sarkkula 2008) but typically about half of the water flowing into the TSLF travels up the Tonle Sap River from the Mekong River, a third flows into the Tonle Sap Lake from its 11 tributaries, and the remainder is from precipitation that falls in the TSLF itself (Kummu et al. 2014).
Habitat change assessment

We assessed habitat change in the Tonle Sap Floodplain over a 25 year period as follows. First, we constructed cloud-free composites of the TSLF for the years 1993, 1998, 2003, 2008, 2013 (all Landsat 7) and 2018 (Landsat 8) for the period January–March, which corresponds to the time of lowest water level in the lake. We used the boundary of the Tonle Sap Biosphere Reserve to define the limits of the floodplain because of its policy relevance. Areas of open water during peak dry-season were defined using data derived from aerial photographs (JICA 2000) and removed from the habitat classification. We then randomly allocated 1,000 points (each 30 m²) to the remaining land area, each separated by a minimum of 150 m, this is equivalent to 0.2% of the area under assessment. For each year under assessment an experienced analyst visually classified vegetation in each point as scrubland, grassland, rice, burnt vegetation, open water, or other (Table 1). The same 1,000 points were used each year. A certainty was assigned to the vegetation classification of each point as follows: 1: uncertain, 2: possible, 3: probable, 4: definite. Although “rice” covers a range of different rice cultivation strategies, dry-season rice makes up at least 70% of cultivated land in the Tonle Sap Floodplain (Ministry of Planning 2018). We did not attempt to identify areas of gallery forest, which is too scarce to be detected using a random sampling approach. Landsat 7 images were viewed using bands 5 (short wave infrared 1), 4 (near infrared) and 1 (blue) to enhance resolution of greens; bands 6, 5 and 2 were used with Landsat 8. Accuracy of habitat assessment was assessed using a reference set of 245 additional points that were ground-truthed in 2013 and 2018 and classified as above from Landsat images for those years.
We used expert analysis and a probability sampling approach rather than a classification algorithm, because unquantified sources of inaccuracy to habitat change estimates can be introduced where spectral characteristics of two (or more) land cover classes are similar (such as rice and grassland) or show high spatio-temporal variation in spectral properties (Olofsson et al. 2014). While a range of remote sensing methods for mapping rice fields have been developed (Dong & Xiao 2016), these methods are confounded by a flood-pulse system and massive spatio-temporal variation in rice cultivation techniques. Point-based visual estimation of land cover classes allowed us to use visual cues that aid identification of similar habitats, while still allowing accuracy to be estimated and uncertainty quantified (Stehman 2013; Olofsson et al. 2014). Landsat data was preferred over radar imagery such as MODIS, despite the difficulties posed by clouds, because the spatial resolution of MODIS is too low relative to the size of rice fields in the TSLF (Mosleh et al. 2015).

**Table 1.** Examples of habitats with sampling point (red circle) used in the analysis.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Description</th>
<th>Example (Landsat 7; 1:25,000)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open water</td>
<td>Even, deep blue</td>
<td><img src="image.png" alt="Image" /></td>
</tr>
</tbody>
</table>
Scrub  Bright green, blotchy appearance due to canopies

Grassland  Smooth purplish green (note scrub patch on bottom edge of image)

Rice  Straight field boundaries, smooth bright green when growing, pink when ploughed (note water and scrub patch in irrigation pond to left of image)

Burned  Dark purple (note that this fire was in grassland, two tiny scrub patches are in the burned area)

Other  Mixed appearance usually with white, pink and pale blue, here the point is located in a village

Data analysis

We removed all points classified as open water or other (270 points), and all points with a certainty of 1 (245 points). Estimates of overall accuracy, producer’s accuracy (a measure of omission error: the probability that reference data are correctly
classified) and user’s accuracy (a measure of commission error: the probability of how well the classified sample represents what is found on the ground) were calculated for points with certainty of 2–4 and 3–4 (Olofsson et al. 2014). For each year under analysis we computed direct estimates of area for each habitat class from the proportion of points identified as belonging within a given class (Stehman 2013), and quantified uncertainty in our area estimates by calculating standard error following (Olofsson et al. 2014). On the basis of this analysis, we only used points with an accuracy of 3 or 4 because estimates of accuracy were higher than when using points with accuracy of 2–4 (overall accuracy 83.5% vs 79.0%, user’s accuracy 83.5% vs 79.1%, producer’s accuracy 71.7% vs 65.2%) (Table S1).

*Trends in anthropogenic fire*

Like (Ashwell 2017), we used a large freely accessible dataset to quantify occurrence of fires in the TSLF between 1 January 2001 and 30 April 2019 using Moderate Resolution Imaging Spectroradiometer (MODIS) Thermal Anomalies / Fire locations data provided by LANCE FIRMS operated by NASA ESDIS (NASA 2019). Standard descriptive statistics obtained included the numbers of ignitions per year and Fire Radiative Power (FRP), which is linearly correlated with biomass consumed, for each individual fire and annually.
To quantify some of the implications of habitat change we used published estimates of fish productivity and carbon storage from different habitats in the TSLF. Published data indicate that fish production (kilos of fish per hectare that are available to be harvested each year) in Cambodia is higher in seasonally flooded scrubland than in grassland and rain-fed rice fields, data are not available for irrigated dry-season rice fields but fish productivity is likely to be lower than in rain-fed rice owing to greater use of agricultural chemicals (Chheng et al. 2016). Estimates of carbon storage derived from standard plot-based sampling techniques indicate that scrubland and grassland in the TSLF contain small amounts of above ground carbon but have large stores of below ground carbon that is lost when habitats are burned and/or ploughed for rice cultivation (MacKenzie et al. 2018). We assumed that these values are consistent across the TSLF and across years, and multiplied them by the area of each habitat class in each year to provide an approximate estimate of trends.

**Results**

**Habitat trends**

We found evidence for dramatic human-induced habitat change in the TSLF during the period 1993-2018 (Table 2). The areal extent of scrubland and grassland declined by 27% during this period from 75% (95% CI: 67–83%) in 1993 to 52% (95% CI: 45–64%) in 2018. Scrubland cover increased slowly between 1993 and 2003, but then increased rapidly to 8,660 km² (7,671–9,650 km²) in 2008, primarily at the expense of grassland (Fig. 3a). Areal extent of scrubland then declined by 22% to 6,776 km²
(95% CI: 5,967–7,586 km²) during the last ten years of the study period owing to
direct conversion to rice (Fig. 2). Prior to 2013 when scrubland began to be cleared
for rice cultivation, scrubland was rarely converted to rice or degraded to grassland
(Fig. 3a).

Loss of grassland has been particularly stark (Fig. 2). In 1993, grassland covered
~23% (95% CI: 19–27%) of the TSLF, however, between 1993 and 2003, the area of
grassland declined by 28% (95% CI: 19–42%), dropping from 3,160 km² (95% CI:
2,596–3,724 km²) to 2,226 km² (95% CI: 1,494–3,030 km²) with conversion to rice
and succession to scrubland responsible for approximately equal amounts of loss (Fig.
3b). Between 2003 and 2013, the rate of grassland loss increased to 20% per annum,
due to direct conversion to rice and succession to scrubland. The rate of grassland loss
declined in the last five years of the study period only because there was very little
grassland left, and in 2018 grassland covered only 4% (95% CI: 0–10%) of the TSLF
(519 km² (95% CI: 0–1,328 km²)).

The area of the TSLF under rice cultivation reflected changes in the other land types:
slight increases over the first 15 years from 3,216 km² (95% CI: 2,652–3,780 km²) to
3,657 km² (95% CI: 2,668–4,647 km²) in 2008, followed by rapid expansion to 6,013
km² (95% CI: 5,204–6,822 km²) in 2018 (Fig. 2). Gains in grassland area during the
early part of the period were mostly at the expense of grassland, but as the area of
grassland declined in later years, rice cultivation began to expand into scrubland areas
(Fig. 3c) Later in the period, land under rice cultivation was rarely allowed to revert to
natural habitats, but between 2003 and 2008 there was significant loss of grassland, mainly to scrubland (Fig. 3c).

Figure 2. Habitat change in the Tonle Sap Floodplain between 1993 and 2018. Solid line is scrubland, dashed line is grassland, and dotted line is rice.
Figure 3. Areal extent of habitats to which (a) scrubland, (b) grassland, and (c) rice lose to or gain from in each time interval. Dark grey is scrubland, pale-grey is grassland, and white is rice.

**Anthropogenic fires**

Excluding the El Niño event of 2016 in which there were 5,426 fires, the mean number of fires year\(^{-1}\) in the TSLF between 2001 and 2019 was 1,288 (SD: 739, range: 197–2,423). Annual variation in FRP and number of fires are highly correlated.
(R² = 0.952). The FRP/fire in 2016 was 54.1, higher than the mean FRP/fire for other years (28.5, SD: 6.3, range 19.9–43.7), indicating that in 2016 a high proportion of fires consumed higher biomass habitats, such as scrubland, or burned for longer.

**Implications of habitat trends for fish productivity and carbon storage**

We estimate that potential fish production in the TSLF rose slightly between 1993 and 2003 to 192,304 Mt/year, but then declined by about 6% between 2008 and 2018 to 187,369 Mt/year as seasonally flooded habitats were replaced by rice fields. Habitat trends documented here indicate that over the past 25 years there has been a reduction in total carbon in the TSLF of approximately 12% to 2018, with most of the losses occurring in the last ten years.

**Discussion**

**Impacts of agricultural intensification on habitats**

Agricultural intensification and expansion has caused a substantial reduction in seasonally flooded habitats in the TSLF, especially over the past ten years. In 1993, grassland and rice each made up approximately a quarter of land cover, but grassland cover declined throughout the study period, initially at a slow rate due to succession to scrubland after cattle grazing was stopped (because novel irrigation infrastructure blocked access to grazing land), and then at a more rapid rate as it was almost completely replaced by rice fields, which by 2018 covered almost half of the TSLF.
Grassland is easy to convert to agriculture and rarely targeted for protection (Parr et al. 2014), as a result, almost all grassland in the TSLF has now been lost to agricultural intensification. Agricultural expansion has accelerated at the expense of scrubland since almost all of the grassland was lost. The increase in scrubland between the mid 1990’s and the late 2000’s (Packman et al. 2013a) was temporary.

Arguably the most important driver of habitat change, beyond changes in either hydrology or climate, has been the political changes in Cambodia over the past 25 years. Political stability was not achieved until around the year 2000 when the Cambodian ruling political party consolidated power (Kelsall & Seiha 2014). Initially, this created opportunities for the locally wealthy to appropriate low-intensity farmland and convert it to irrigated dry-season rice. At the same time, the government developed sector-specific policy that encouraged agricultural intensification, starting with the 2004 National Export Strategy for rice that referred to “rice – white gold”, which was followed in 2010 by a Prime Ministerial level “Policy Paper on the Promotion of Paddy Production and Rice Exports” that set out how to “turn Cambodia into a “rice basket” and a major rice-exporting country in the global market” (Royal Government of Cambodia 2010). In order to reach an export target of 1 million tons by 2015 (up from 12,600 in 2009), the policy paper set out a three-pronged strategy with construction, expansion and improvement of irrigation infrastructure as the first priority. Irrigation allows farmers to cultivate two or three crops of rice per field per year, increasing the economic incentive to clear seasonally flooded habitats. A flow of foreign aid and investment and a significant increase in national budget allocations has enabled construction of industrial-scale irrigation infrastructure (Godfrey et al. 2010).
2002), which has facilitated cultivation of dry-season rice as a cash crop by almost all farmers in the TSLF (Ibbett et al. 2019).

To date, the future impacts of hydropower development in the Mekong Basin and climate change have dominated the discussion regarding habitat trends in the TSLF because the published predictions are so dramatic (Arias et al. 2019). Up to 187 hydropower dams have been built or are planned, including up to 11 mainstream Mekong dams in Lao PDR and Cambodia (Grumbine & Xu 2011; WLE-Mekong 2020). Hydropower development up to 2030/2040 is likely to dampen the Tonle Sap annual flood reversal (Hecht et al. 2019). The reversal may cease altogether if the flood pulse is dampened by $> 50\%$ and delayed by one month, which is possible under some hydropower development scenarios (Pokhrel et al. 2018). Between 2010 and 2040, the implications of this are that the area of seasonally flooded habitats is predicted to decline by 1,300 km$^2$, increasing the area suitable for agriculture (Arias et al. 2012; Arias et al. 2013), with significant impacts on animal species with ecological, nutritional or conservation value (Arias et al. 2014). Here we have shown that between 2008 and 2018 alone, approximately 2,300 km$^2$ of seasonally flooded habitat was lost to agriculture, with another 400 km$^2$ recently burnt that, based on our observations, is likely to be cultivated in the near future.

**Impacts of people on habitats in the TSLF**

Twelve hydropower dams have already been built on the Mekong and hundreds more on its tributaries upstream of the TSLF in the Mekong Basin (WLE-Mekong 2020).
The recent locally driven agricultural expansion and concomitant loss of seasonally flooded habitat may be partly a consequence of, and further exacerbated by, changes to the hydrology of the TSLF due to hydropower, as well as to the impacts of climate change on local weather conditions. Between 2000 and 2010, hydropower dams had already dampened the Tonle Sap flood pulse by at least 10%, with the annual average open water area thought to have decreased at a rate of 25.3 km²/year (Cochrane et al. 2014; Lin & Qi 2017), making cultivation of traditional deep-water rice varieties impossible in some areas and increasing opportunities to cultivate dry-season rice closer to the permanent lake-edge. At the same time, Cambodia’s climate is warming, with the greatest rate of temperature increase during the hottest, driest months (March-May) (Thoeun 2015), making it easier for farmers to set fires to clear scrubland for rice cultivation. Cambodia’s temperature is projected to rise by 0.7–2.7 °C by the 2060s, and 1.4–4.3 °C by 2090 (Thoeun 2015). These values were exceeded during the 2016 El Niño event, during which Cambodia experienced land surface temperature anomalies of up to 6 °C in April (Thirumalai et al. 2017) and there was a massive increase in the number of fires in the TSLF (Ashwell 2017), which has not been sustained in subsequent years with normal temperatures. The frequency of El Niño events is also predicted to increase as the climate warms (Cai et al. 2014), so Cambodia is likely to experience a greater frequency of years with temperatures similar to 2016 (Thirumalai et al. 2017). As Cambodia warms and becomes drier it is likely that people will increasingly take advantage of the hot and dry conditions to burn and clear remaining scrubland in the TSLF to plant rice.
Implications of habitat change in the TSLF

The impacts of agricultural intensification in the TSLF on net loss of carbon/hectare due are similar to those reported for conversion of tropical forests that lack significant stores of below ground carbon (Warren-Thomas et al. 2018). The natural vegetated ecosystems surrounding the TSFL play an important role in climate change adaptation and mitigation (Mitsch et al. 2013). The flood pulse delivers and deposits carbon rich sediments and organic matter to these vegetated areas during the wet season that, coupled with plant productivity, means the seasonally flooded habitats have high stocks of carbon (MacKenzie et al. 2018). Conversion of these systems to rice fields through burning not only reduces the ability of these systems to sequester additional CO₂ but also converts them from a sink to a major source of greenhouse gas emissions.

Our overall estimates of fish productivity in the TSLF are broadly similar to published figures for the annual fish catch (Van Zalinge 2002). However, the impacts of scrubland clearance on fish populations are unlikely to be linear because seasonally flooded scrubland is an important nursery ground for many fish species. Our conclusions about impacts of locally-driven habitat change on food security also overlook important spatial variation in fish abundance, fishing effort and catch size within the TSLF, but nonetheless overall trends correlate with the perceptions and experience of communities living in the TSLF (Althor et al. 2018). Impacts of reduced fish productivity are typically greatest for the rural poor (Baran & Myschowoda 2009; Ziv et al. 2012), indeed almost all people in the TSLF rely on wild-caught fish to some degree, even if they do not identify as fishers (Nasielski et
al. 2016). These communities cannot afford to replace wild-caught fish with other sources of farmed animal protein (Vilain et al. 2016), as has been suggested (Orr et al. 2012), while a switch to farmed fish would encourage the indiscriminate capture of small (often juvenile) fish to feed the farmed fish (Naylor et al. 2009).

We are not able to make specific inferences on the impacts of habitat change on aquatic biodiversity. Although some of the fish species in the TSLF are globally threatened (IUCN 2019), spatio-temporal patterns in their use of the lake and its habitats are complex and incompletely known (Lim et al. 1999; Kong et al. 2017; Pool et al. 2017). For impacts of agricultural intensification on terrestrial biodiversity, we highlight the rapid decline of the Bengal Florican, which relies on floodplain grassland or low intensity agriculture such as deep-water rice (Gray et al. 2007). The TSLF population of Bengal Florican, which constitutes the entire global population of the subspecies *H. b. blandini*, has declined by c.11% per year since 2005 and now numbers only 104 (95% CI: 89–117) displaying males in four sites (Mahood et al. 2019).

Conclusions and recommendations

As they have for millennia, local scale human activities continue to shape the vegetation and ecosystem services provided by the TSLF. We have shown that between 1993 and 2018, habitat has already changed as a result of agricultural expansion and intensification more than published predictions of the impacts of hydropower and climate change between 2010 and 2040, a rate of loss of seasonally
flooded habitats that is increasing. Thus, whilst hydropower on the Mekong River and climate change have attracted greatest attention as risks to the TSLF, immediate existential threats to the remaining natural habitats are being driven by the response of local communities to economic opportunities combined with supportive government agricultural policies. While we do not advocate ignoring the future implications of hydropower dams and climate change, the habitat trends that we have documented, and the declines in fish stocks that we think likely to have occurred as a result, greatly threaten food security and biodiversity today.

We propose four measures to address the issues identified here, which would also help to mitigate against published predictions of the impacts of hydropower and climate change in the TSLF. Firstly, areas that are already zoned for protection, such as the three Core Areas of the Tonle Sap Biosphere Reserve, the Northern Tonle Sap Protected Landscape, the 58 Fish Sanctuaries and Zone 3 must be strictly protected and/or restored so that they can provide ecosystem services to the surrounding communities and protect key populations of both fish and other threatened species. Existing laws must be enforced, and training and equipment given to relevant government agencies. Consideration should also be given to increasing the area of seasonally flooded habitats under strict protection in Pursat and Kompong Thom provinces where populations of threatened species have persisted to date outside protected areas. Secondly, Community Fisheries should be better supported to manage their fisheries sustainably, particularly by protecting seasonally flooded habitat. Third a campaign across the TSLF should be implemented to reduce the incidence of fires where these are likely to be damaging fish stocks and biodiversity. Lastly, relevant
government agencies, investors and development agencies should thoroughly screen irrigation and infrastructure plans using relevant legislation (including the recent Environmental Impact Assessment Law) for direct and induced impacts on seasonally flooded habitats, and reconsider projects or develop suitable mitigation measures. Without urgent, coordinated action to address local-scale drivers of habitat change in the TSLF, the ecosystem that has sustained Cambodia for generations may be lost.

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**Compliance with Ethical Standards**

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

Data Availability: The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.
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Table S1. Assessment of accuracy for vegetation classification using three measures of accuracy, for each vegetation class and all vegetation classes combined.

<table>
<thead>
<tr>
<th>Vegetation Class</th>
<th>Users (%)</th>
<th>Producers (%)</th>
<th>Overall (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scrubland</td>
<td>81.3</td>
<td>46.4</td>
<td>71.1</td>
</tr>
<tr>
<td>Grassland</td>
<td>83.6</td>
<td>83.6</td>
<td>83.5</td>
</tr>
<tr>
<td>Rice</td>
<td>84.2</td>
<td>72.7</td>
<td>83.5</td>
</tr>
<tr>
<td>All</td>
<td>83.5</td>
<td>71.7</td>
<td>83.5</td>
</tr>
</tbody>
</table>
Chapter 6.

IUCN captive management guidelines support ex situ conservation of Bengal florican *Houbaropsis bengalensis blandini*

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Bengal Florican, Bustard, Captive management, Decision tree, Demographic modelling, Ex situ conservation, Extinction, IUCN guidelines

Abstract

Ex situ conservation of species is risky and sometimes expensive, but it can prevent extinction when in situ conservation fails. We used the IUCN Guidelines on the “Use of Ex situ Management for Species Conservation” to evaluate whether to begin ex situ conservation for the Southeast Asian subspecies of Bengal Florican Houbaropsis bengalensis blandini, which is predicted to be extinct in the wild within five years. To inform our decision, we used a demographic model to evaluate probability of establishing a captive population under a range of husbandry scenarios and egg harvest regimes, and compared this with the probability of persistence for the wild population. The model showed that if ex situ conservation draws on international best practice in bustard husbandry then there is a high probability of establishing a captive population, but the wild population is very unlikely to persist. We identified and evaluated the practical risks associated with ex situ management, and document our plans to mitigate them. Modelling shows that it is unlikely that birds could be released within 20–30 years, by which time genetic, morphological and behavioral changes in the captive population, combined with habitat loss and extinction of the wild population, make it unlikely that H. b. blandini can be released into a situation approximating their current wild state. We considered the philosophical and practical implications through a decision tree so that our decision to begin ex situ management is not held back by our pre-conceived notions of what it means to be wild. We believe
that the decision tree that we developed would be a useful tool for any group considering *ex situ* conservation of a species.

**Introduction**

*Ex situ* management is an increasingly common tool for preventing extinctions of species (Seddon et al. 2007; Redford et al. 2011), with 34 animals and 35 plants classified as Extinct in the Wild and so relying entirely on persistence of populations in captivity (IUCN 2019). Successful case studies are well known in the conservation community, spanning North America (e.g. California Condor *Gymnogyps californianus*), Asia (e.g. Crested Ibis *Nipponia nippon*), Indian Ocean islands (e.g. three Mauritius endemic bird species) and the Pacific (various bird species endemic to New Zealand) (Snyder & Snyder 2000; Xi et al. 2002; Edmunds et al. 2008; Jones & Merton 2012). The hope that they engender coupled with the dire situation facing an increasing number of species in the wild (Butchart et al. 2010), manifests in recommendations for captive breeding in the IUCN Red List accounts of 2,199 threatened or Near Threatened species (IUCN Conservation Planning Specialist Group 2019). However, zoos can conserve only a small proportion of threatened species (Balmford et al. 1996), and the familiarity of successful case studies masks the fact that *ex situ* management is difficult, risky, time-consuming and financially costly, and can increase the risk of extinction for wild populations (Snyder et al. 1996). A global evaluation of reintroductions found that only 13% were successful when the source population was captive, and all reintroductions fail when the threat that caused the decline is not removed (Fischer & Lindenmayer 2000). Faced with data that indicates a rapidly declining population, conservation managers must make a
timely, informed decision regarding whether or not to proceed with \textit{ex situ}
management (McGowan et al. 2017). A failure to act quickly on available evidence of
species declines can lead to extinctions (Martin et al. 2012), but making the wrong
decision can also increase the risk of extinction (Snyder et al. 1996).

Management of species occurs along a continuum of states ranging from free-ranging
self-sustaining wild populations to species that now exist only in captivity (Redford et
al. 2011). Lines between states are increasingly blurred due to the increase in \textit{ex situ}
management (Redford et al. 2012) and the variety of \textit{ex situ} management regimes
from small cages to extensive semi-natural environments. We follow the intuitive
definition in (IUCN/SSC 2014) under which \textit{ex situ} is defined as conditions under
which individuals are “the individuals are maintained in artificial conditions under
different selection pressures than those in natural conditions in a natural habitat”.

Duration of time in \textit{ex situ} conditions can vary from short, for example during
temporary removal of a population during predator control, to indefinite, for species
for which there is no hope of reintroduction in the foreseeable future. \textit{Ex situ}
management has a range of purposes, including conservation, re-stocking for sport,
and education (Fischer & Lindenmayer 2000). Here we consider only captive
breeding for preventing extinctions of species, for which we use the term ‘\textit{ex situ}
conservation’. The ultimate goal of \textit{ex situ} conservation is the re-stocking or re-
establishment of wild populations, which distinguishes it from capture solely to
establish captive populations for display, education, farming or private enjoyment.

For this reason, individuals maintained and bred in captivity should be capable of
producing descendants that can survive in the wild. Ideally, where possible, a parallel
program of in situ conservation should ensure that populations are maintained in the wild which birds released from captivity can augment. However, ex situ conservation can inadvertently compromise source populations by removing too many individuals (increasing rates of decline), or distracting decision makers such as governments and funders to the detriment of in situ conservation (Snyder et al. 1996). The IUCN guidelines suggest that success of in situ conservation should not be unduly jeopardized by ex situ conservation (IUCN/SSC 2014) unless conditions in the wild are so hostile that the ex situ conservation plan requires that the entire wild population is taken into captivity (McCleery et al. 2014).

Ex situ conservation can buy time for conservation managers to eliminate introduced predators, restore habitat or enact legislative changes that create conditions for species to survive in a wild state (Andrew et al. 2018), but it must begin when there are sufficient wild individuals to establish a captive population. Species whose extinction might otherwise have been prevented, such as a number of reptiles and a bat endemic to Christmas Island, and the Po'ouli Melamprosops phaeosoma, were lost because plans for ex situ conservation were not enacted until too few individuals remained (VanderWerf et al. 2006; Martin et al. 2012; Andrew et al. 2018). Although most risks emanating from ex situ conservation can be mitigated, this is costly and time-consuming and none can be prevented entirely. However, avoidance of decisions about ex situ conservation due to perceptions of risk, fear of failure, and fear of being perceived to have made the wrong decision is itself a decision to do nothing (Brook et al. 2014) which can itself lead to extinctions (Woinarski et al. 2017).
The IUCN has developed guidelines to help conservation managers determine how and when *ex situ* management should be used in conservation (IUCN/SSC 2014). The guidelines provide a logical five step decision-making process that finishes with a call to make a decision that is informed by the information gathered in the preceding four steps and “weighing the potential conservation benefit to the species against the likelihood of success and overall costs and risks of not only the proposed *ex situ* program, but also alternative conservation actions or inaction” (IUCN/SSC 2014; McGowan et al. 2017). Step 1 is a review of the status of the species, in step 2 the role(s) that *ex situ* management could play in the conservation of the species is defined, step 3 is an evaluation of the precise nature of the desired *ex situ* population in order to meet the identified role(s), and in step 4 resources, expertise, feasibility and risks are appraised (McGowan et al. 2017). There is no method proposed for the critical fifth step, which is to make a decision on whether to initiate captive breeding. Because captive breeding for conservation can be risky and controversial, decision making should be conducted using a method that enables wide participation in the process so that practitioners ‘own’ the results rather than feeling disempowered by top-down systems of management (Black et al. 2011). Hidden value judgements can be revealed and managed by following a transparent process that documents why and how decisions were made, with uncertainty acknowledged and quantified where possible so that it can be incorporated into the decision-making process (Game et al. 2013). However, without the aid of tools, people struggle to quantify risk in decision making processes (Redford & Taber 2000). The tool used most commonly for structured decision analysis in conservation is the decision tree (Maguire 1986). Decision trees have been used to choose between *ex situ* conservation and other options to varying
degrees of success, but when a species is under imminent threat of extinction in the wild the chance of success for any conservation plan is low (Regan et al. 2005).

Although (IUCN/SSC 2014) calls for dissemination of information regarding use of the guidelines, we can find no published papers that explicitly document their use. Here, we have applied the IUCN Guidelines on the “Use of Ex situ Management for Species Conservation” (IUCN/SSC 2014), taking as a case study the Southeast Asian subspecies of Bengal Florican *Houbaropsis bengalensis blandini*, a critically endangered bustard now restricted to Cambodia (BirdLife International 2018b). Since the mid 2000’s (the date of the first reliable population data), *H. b. blandini* has experienced a decline of >10% per annum that shows no sign of abating (Gray et al. 2009; Packman et al. 2013b; Mahood et al. 2019), owing to habitat loss, agricultural intensification, hunting and predation by free-ranging domestic dogs (Packman et al. 2013a; Ibbett et al. 2019). In 2018 the population was estimated at 138 (95% CI: 119–156) birds at four sites where display activity still occurs, and one site (Koup Preah Buong Treang) where a few additional birds remain (Mahood et al. 2019). Intensive in situ conservation efforts stabilized population trends at one site, Stoung-Chikreang Bengal Florican Conservation Area (BFCA) (Mahood et al. 2019), but that population is now threatened by a newly-constructed power line that could lead to local extinction (Mahood et al. 2016). Given the dire situation facing *H. b. blandini* there have been calls from within Cambodia to consider captive management to prevent its extinction (M. Meyerhoff *pers. comm.*). Mindful of the need to make a timely decision on whether to proceed with captive management, but aware of the potential risks of making the wrong decision, we use demographic modelling to explore the
consequences of \textit{ex situ} conservation and support rational decision-making (Addison et al. 2013). Using the principles of decision science, we have adapted the guidelines so that the issues for consideration under steps 2–4 create tools (including a decision tree) that fulfil the requirements of the decision-making required in Step 5. We believe that these augment (McGowan et al. 2017) who provided additional guidance on use of the IUCN/SSC guidelines but not tools or a worked example. We show how these tools enabled us to make a decision about \textit{ex situ} conservation of \textit{H. b. blandini} and hope that they will assist conservation managers facing similar predicaments.

Methods

\textit{Development of tools}

We first conducted a status review of \textit{H. b. blandini} (Mahood et al. 2019), following Step 1 of the guidelines (IUCN/SSC 2014). We created a decision tree that combined Step 2 (identification of the potential role for \textit{ex situ} conservation in the conservation of the species) with the part of Step 4 that evaluates risk to the wild population from \textit{ex situ} conservation (Fig. 1). A simple table was created so we could evaluate the practical considerations associated with \textit{ex situ} conservation of \textit{H. b. blandini} (Table 1: Step 3), and a similar table created so that we could evaluate practical risks (Table 2: part of Step 4). The practical risks were separated from risks to the wild population because they can be mitigated, unlike biological risks for which mitigation is often difficult or impossible.
Figure 1. Step 2 and 5: decision tree to allow conservation managers to determine the kind of ex situ management required, and consider biological risks associated with ex situ management of species. Dashed arrows indicate the consensus of the group in the example discussed in this paper.

Demographic modelling

To inform our evaluation of practical and biological risks to the wild and captive populations (Step 4), and evaluate whether ex situ management would increase the chance of persistence for *H. b. blandini*, we used a demographic model developed for evaluating the efficacy of captive breeding for Great Indian Bustard *Ardeotis nigriceps* (Dolman et al. 2015). See links in that publication for publicly available R
code used here. We retained the same parameters as (Dolman et al. 2015), except where data existed for Bengal Florican or the more similarly-sized little bustard *Tetrax tetrax*, or where variation was expected based on body size (Supplementary Information Table S1 and S2). Sensitivity to variation in parameters was evaluated by sampling parameter values from four scenarios of efficacy of *ex situ* conservation (below average, above average, best possible and full range) and two scenarios of *in situ* conservation (current situation and future conservation). See (Dolman et al. 2015) for detailed methodology, only key points are summarized here. Analysis was conducted in R version 3.5.1 (R Core Team 2018). Where we differ most from Dolman et al. (2015) is in the nature of the situation with which we compare captive breeding. Dolman et al. (2015) compared the effect on the wild population of either pursuing a program of captive breeding and subsequent release, or increasing efforts to improve conservation of bustards in the wild in the absence of *ex situ* conservation. Under our comparison, we believe that we are currently doing all that is possible to maintain the wild population, but that in light of population trends, habitat trends and emerging threats to the remaining populations (Mahood et al. 2019), rates of adult survival of wild birds is likely to decline. Consequently, whilst parameters used to define future scenarios for *in situ* populations by (Dolman et al. 2015) were mostly higher than those for the current situation, we are persuaded that they should be lower for Bengal Florican in Cambodia.

The model allowed us to evaluate the chance of persistence of a captive *H. b. blandini* population under various strategies for collecting eggs from the wild, and the probability that individuals could be released within 50 years. Twelve years of
population monitoring indicates that *H. b. blandini* will be functionally extinct by 2023 (Mahood et al. 2019). The captive breeding model assumes that we can collect a maximum of five or ten eggs in the first year, but that this will decline by 2 eggs per year for five years as the wild population declines (until 2023). We did not model collecting adults from the wild because the group rejected this as a method owing to the risk of mortality of birds during capture, which was judged likely to cause the government to immediately close the *ex situ* conservation program. The release model assumes that all released birds are less than one year of age to minimize behavioral adaptation to captivity (Inchausti & Bretagnolle 2005). Releases do not occur until after the captive population has reached 20 mature females so that they do not jeopardize the persistence of the captive population (IUCN/SSC 2013), and the group size of released birds is five because this is minimum that might constitute a population (four males to form a lek plus one female) (Gray et al. 2009), although releases can occur in multiple years. For captive management models, we considered four scenarios of performance quality to account for variation in demographic performance of captive management, namely ‘full range’ (taking in the full range of values for all parameters), ‘below average’ (only using below average values for all parameters), ‘above average’ (using only above average values for all parameters) and ‘best possible’ (using only the highest values for all parameters), and accounted for the impacts of stochastic events; parameters contained in Table S1; for methodological details see (Dolman et al. 2015). Outcomes of the captive breeding programme were assessed against the proportion of 1,000 model runs extirpated by year 50, whether they provided surplus individuals for release, and numbers of breeding age birds established in the wild following (Dolman et al. 2015).
Assessment process

All relevant stakeholders took part in application of the IUCN guidelines for assessment of the potential role of ex situ management for H. b. blandini at a meeting held in April 2019, Phnom Penh, Cambodia; all are co-authors on this paper. Stakeholders included representatives from the relevant government ministries (Ministry of Environment and the Forestry Administration of Ministry of Agriculture, Forestry and Fisheries), the only non-governmental organization working on conservation of H. b. blandini (Wildlife Conservation Society: WCS), and the captive facility that had expressed interest in ex situ management of H. b. blandini (Angkor Centre for the Conservation of Biodiversity: ACCB). Presentations were given to summarize the results of the H. b. blandini status review (Step 1) and the demographic modelling described here. Participants worked through the first part of the decision tree to identify the role that ex situ management could play in H. b. blandini conservation (Step 2). Presentations were given on case studies of ex situ conservation successes and failures, the facilities at ACCB, and ex situ conservation of bustards worldwide. Tables of practical considerations (Step 3) and practical and logistical risks (Step 4) were populated in advance with issues for consideration using (IUCN/SSC 2014). Participants were also invited to identify additional issues which were added to the tables. The whole group assessed the biological risks associated with ex situ management using the decision tree (Step 5) for the population of H. b. blandini as a whole, and for each of the four remaining sub-populations. Results were summarized by the facilitator. A basic plan for ex situ management of Bengal Florican was developed based on the outcome and outputs of the meeting (Step 5).
Results

Using the decision tree (Fig. 1), the group decided to proceed with *ex situ* management of *H. b. blandini*, despite the risks, because of rapid declines in the wild population (which may be accelerating), and the likelihood that threats could not be controlled in the wild before the taxon was rendered extinct. The demographic modelling that was used to inform decision making indicated that there is a 40% probability of captive population extirpation within 50 years under the ‘above-average’ scenario at egg harvest rates of 5 yr\(^{-1}\) for 5 years, this rapidly drops to 17% if harvest rates are 10 yr\(^{-1}\) (Fig. 2). For the ‘best possible’ scenario, probability of captive program extirpation is only 12% at egg harvest rates of 5 yr\(^{-1}\) for 5 years. The group considered that it was likely that harvest rates would be between 5 and 10 eggs per year, but given the rate of decline of the wild population it was unlikely that harvest could continue beyond five years.
Figure 2. Captive demography for three scenarios of programme quality (1: ‘full range’; 2: ‘above average’; 3: ‘best possible’) and two rates of egg harvest (5 or 10 eggs yr⁻¹, both for 5 years), with and without removal of birds from the captive population for reintroduction, with probability of extinction of the ex situ programme after 50 years (ppe); black line shows the geometric mean of model runs.

Under the ‘below average’ scenario for ex situ conservation of H. b. blandini, the captive population is never successfully established, whilst under the ‘full-range’ scenario there is an 83% chance of extirpation within 50 years (at egg harvest rates of 5 yr⁻¹ for 5 years). In this context, identification and mitigation of practical risks
associated with *ex situ* conservation of *H. b. blandini* is critical to ensure that real-world parameters match those in the ‘above-average’ or ‘best possible’ scenarios. Of the two risks that we rated ‘high’ (Table 2), refusal of governmental permission to collect eggs was managed by beginning to request permits before the assessment as a precautionary measure given the time constraints. This risk was rated ‘high’ because permission had not been granted at the time of the assessment and *ex situ* conservation simply cannot start without it, however, permission to harvest and transport eggs has since been granted. We rated risks associated with harvest of eggs from the wild as ‘high’ because nests will have to be found by community members, and it is impossible to eliminate the possibility that community members will misunderstand instructions and take eggs to their homes (rather than leaving them in the nest) in an attempt to assist the project. We also considered rating knowledge of husbandry techniques relevant to *H. b. blandini* as ‘high’ because the species has so rarely been kept in captivity. Good husbandry should aim to minimize adult mortality, because sensitivity analysis showed that probability of captive population extirpation was most heavily impacted by changes in adult mortality (Supplementary Figure S1). In our risk assessment we noted that there is considerable global expertise in *ex situ* management of other bustard species on which we can draw, and we have already begun receiving technical advice from a number of bustard breeding facilities.

Demographic modelling indicates that there is little chance that *ex situ* management will produce a sufficient number of *H. b. blandini* to reintroduce birds within 50 years (Fig. 3). Even under the ‘best possible’ scenario with egg harvest rates of 10 yr⁻¹ for 5 years, there are unlikely to be sufficient birds to release for 20–30 years, by which
time *H. b. blandini* will almost certainly be extinct in the wild. Participants considered this information as they worked through the decision tree to assess biological risks associated with *ex situ* management (Fig. 1), but concluded that, given the relatively low risk of extirpation of a well-managed captive population and the very high risk of extirpation of the wild population, embarking on a program of *ex situ* management was urgent and crucial to avoiding extinction altogether (Fig. 3).

**Figure 3.** Numbers of free-living adult females established by captive breeding and release (‘released pop’: dark lines) or by a strategy of in situ conservation only (‘counter pop’: pale lines) alive in each programme year, 1 to 50, under two different scenarios of in situ conservation: current situation (CS1), likely future situation (CS2). Probability of extinction of the ex situ programme after 50 years (ppe) and percentage of model runs under which no birds were able to be released are given (failure to release). For details see Dolman et al. (2015).
Based on the assessment of risks described above, the participants re-visited Table 1 and 2, and used them to develop a plan for *ex situ* management of *H. b. blandini* (Table 3), which is summarized here. Contingent on government permission, as many eggs as possible will be harvested from the unprotected population at Sankor in the 2019 breeding season (April–September), which is declining extremely rapidly and is likely to be extirpated within a year because the habitat has been transformed from grassland to rice (Table 3). At all sites, any eggs laid during July or later will be harvested, because it is thought that these represent late or second breeding attempts that are highly likely to fail due to heavy rain and rising floodwater. Mortality caused by the power transmission line (completed in March 2019) that bisects the stable, protected, population at Stoung-Chikreang BFCA will be monitored throughout the 2019 and 2020 breeding seasons. If significant mortality is detected, then all eggs will be harvested in the following year. If low mortality is detected, then a decision will be made on whether to begin harvesting all eggs in the 2020 breeding season. Eggs will be collected from any nests found in Sankor in 2020. Improvements to the *in situ* conservation program at the protected population in Baray BFCA were made in early 2019, this population will be monitored intensively, and if signs of decline are detected then a decision will be made on whether to take eggs. The tiny population at Bakan will be left in the wild because efforts to harvest eggs are best directed towards locations with more individuals and there is still potential for this population to persist if an application to protect this site is successful. Samples will be taken from all captive individuals for molecular genotyping to determine relatedness so that we can design a captive breeding program that maximizes fitness of offspring (Hogg et al. 2018).
Table 1. Step 3: evaluation of biological and practical considerations associated with ex situ conservation of *H. b. blandini*.

<table>
<thead>
<tr>
<th>Considerations</th>
<th>Desired state</th>
<th>Likely state</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Required number of founders</strong></td>
<td>Harvest 5–10 eggs per year for at least 5 years</td>
<td>Harvest as many eggs as possible from doomed populations; harvest eggs only from July onwards from populations with a hope of persistence</td>
</tr>
<tr>
<td><strong>Number of individuals to be maintained ex situ</strong></td>
<td>&gt;20 breeding age females, more if possible</td>
<td>83% chance that this can be achieved under ‘above-average’ scenario</td>
</tr>
<tr>
<td><strong>Likely duration of ex situ program</strong></td>
<td>&gt;50 years: under ‘above-average’ scenario minimum of 30 years needed until <em>ex situ</em> population is established (Fig. 2)</td>
<td>60% chance that this can be achieved under ‘above-average’ scenario if 5 eggs year(^{-1})</td>
</tr>
<tr>
<td><strong>Relative risk of behavioral adaptation to ex situ conditions</strong></td>
<td>Moderate, managed through handling protocols and cage design</td>
<td>High, behavioral adaptation to captivity is initially desirable to minimize adult mortality, birds bred for release will be managed differently to minimize adaptation</td>
</tr>
<tr>
<td><strong>Inbreeding</strong></td>
<td>Moderate, managed through maximizing the number of founders, genetic testing of all individuals and planned mating through use of a studbook</td>
<td>Moderate, managed as in the desired state</td>
</tr>
<tr>
<td><strong>Disease management</strong></td>
<td>Single species facility with stringent quarantine procedures</td>
<td>Captive facility only keeps species that originate from Cambodia, standard quarantine and disease risk reduction procedures are in place</td>
</tr>
<tr>
<td><strong>Plans for a release/reintroduction</strong></td>
<td>Only at such a time that it does not jeopardize the captive population</td>
<td>Unlikely to be possible before 2050, when it is impossible to predict suitability of wild conditions</td>
</tr>
<tr>
<td>Considerations</td>
<td>Desired state</td>
<td>Likely state</td>
</tr>
<tr>
<td>------------------------------------</td>
<td>-------------------------------------------------------------------------------</td>
<td>-------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Egg harvest method</td>
<td>Close supervision of search teams by ACCB and WCS staff</td>
<td>Local people asked to report nests to WCS, eggs harvested from nests by ACCB staff</td>
</tr>
<tr>
<td>Geographic location of facility</td>
<td>Proximate to native range (cannot locate inside breeding range of Bengal Florican owing to seasonal flooding)</td>
<td>Proximate to native range</td>
</tr>
<tr>
<td>Nature of facility</td>
<td>Single species</td>
<td>Multi-species, located at Angkor Centre for Conservation of Biodiversity (ACCB), an animal rescue, rehabilitation and captive breeding center managed by Allwetterzoo Münster</td>
</tr>
<tr>
<td>Design of facility</td>
<td>Large enclosures with ample space for flying replicate wild conditions</td>
<td>Small enclosures, breeding and non-breeding birds kept separately, birds not encouraged to fly for fear of injury. Priority given to minimizing mortality.</td>
</tr>
<tr>
<td>Equipment</td>
<td>State of the art</td>
<td>All necessary equipment, and backup equipment, has been purchased and is ready to use</td>
</tr>
<tr>
<td>Staff numbers and skills</td>
<td>Dedicated Bengal Florican staff team</td>
<td>Dedicated bird keeper and veterinarian, Florican staff will not work on husbandry of other bird species to minimize disease risk</td>
</tr>
<tr>
<td>Marking of individuals</td>
<td>Colour rings and microchips on all birds, database (Species360) and stud book kept up to date</td>
<td>As desired state</td>
</tr>
<tr>
<td>Behavioral management</td>
<td>Birds handled as infrequently as possible</td>
<td>Birds for captive breeding will be habituated when chicks to facilitate easy handling and reduce mortality</td>
</tr>
<tr>
<td>Level of public display</td>
<td>Birds not on public display</td>
<td>Birds not on public display, all visitors to the facility will be escorted by staff</td>
</tr>
</tbody>
</table>
Table 2. Step 4: evaluation of logistical and practical risks associated with ex situ conservation of *H. b. blandini*.

<table>
<thead>
<tr>
<th>Risk area</th>
<th>Present situation</th>
<th>Score</th>
<th>How risk is mitigated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Harvest of eggs from the wild</td>
<td>Community members who find nests may misunderstand and take eggs to their homes before reporting them</td>
<td>High</td>
<td>Clear protocol developed, WCS community staff communicate clearly and frequently with local people and ACCB</td>
</tr>
<tr>
<td>Transportation of eggs</td>
<td>One vehicle with portable incubator run from car engine</td>
<td>Low</td>
<td>Vehicle always kept ready for use, facility is located &gt;2 hours drive from breeding grounds</td>
</tr>
<tr>
<td>Equipment</td>
<td>One incubator and foster chickens available, no other specific equipment needed</td>
<td>Low</td>
<td>Keep equipment well maintained</td>
</tr>
<tr>
<td>Facilities and infrastructure</td>
<td>Temporary enclosure constructed with four compartments</td>
<td>Medium</td>
<td>Facilities adequate for short term, in medium term upgrade and expand existing facilities</td>
</tr>
<tr>
<td>Staff numbers and skills</td>
<td>Sufficient staff with experience of keeping birds, experience of care for one adult Bengal Florican</td>
<td>Low</td>
<td>Maintain staff at current levels</td>
</tr>
<tr>
<td>Husbandry techniques</td>
<td>Species has never been kept in captivity for more than three months</td>
<td>Medium</td>
<td>Ongoing technical support is available from staff at other facilities with significant experience in husbandry of bustards</td>
</tr>
<tr>
<td>Food availability</td>
<td>Insects widely sold for human consumption in Cambodia, cricket breeding farm in Phnom Penh</td>
<td>Medium</td>
<td>Purchase crickets from cricket farm, in medium term develop on-site cricket or insect breeding farm</td>
</tr>
<tr>
<td>Spread of disease to wild population</td>
<td>Captive facility is well outside the species range</td>
<td>Low</td>
<td>N/A</td>
</tr>
<tr>
<td>Risk area</td>
<td>Present situation</td>
<td>Score</td>
<td>How risk is mitigated</td>
</tr>
<tr>
<td>----------------------------------------------------</td>
<td>-------------------------------------------------------------------------------------------------------------</td>
<td>-------</td>
<td>-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Spread of disease within captive facility</td>
<td>Costs prohibit building and staffing a single-species facility, rescued birds of other species are a disease risk at ACCB</td>
<td>Medium</td>
<td>Follow standard quarantine protocols, restrict staff movements between Bengal Florican cages and other species</td>
</tr>
<tr>
<td>Catastrophes (e.g. fire (and smoke inhalation), wind, war)</td>
<td>Facility is located in a tropical climate an area with frequent fires</td>
<td>Medium</td>
<td>Fire break constructed around facility; fire-fighting service unlikely to travel to facility but there is basic fire-fighting equipment on site</td>
</tr>
<tr>
<td>Theft of birds</td>
<td>Low value species</td>
<td>Low</td>
<td>Monitor situation</td>
</tr>
<tr>
<td>Revenge attack on facility</td>
<td>No reason to suspect an attack is likely, but possible within cultural context</td>
<td>Low</td>
<td>Monitor situation</td>
</tr>
<tr>
<td>Financial resources</td>
<td>Sufficient for small-scale start up</td>
<td>Medium</td>
<td>Fundraising ongoing targeting sources that would not fund <em>in situ</em> conservation; project will be promoted widely</td>
</tr>
<tr>
<td>Clarity of taxonomy</td>
<td>All birds in source areas are the same taxon</td>
<td>Low</td>
<td>Birds will not be obtained from outside of Cambodia</td>
</tr>
<tr>
<td>Legal requirements (e.g. permits)</td>
<td>Permits do not exist for facility</td>
<td>High</td>
<td>Government staff in the recovery team will assist with obtaining permits to harvest eggs from wild birds and transport them to the facility</td>
</tr>
<tr>
<td>Lack of collaboration between government and non-government stakeholders</td>
<td>Bengal Florican Recovery Team has government and non-government members</td>
<td>Low</td>
<td>Add stakeholders to team as needed</td>
</tr>
<tr>
<td>Health and safety of people</td>
<td>Species does not pose a direct risk to people</td>
<td>Low</td>
<td>All adults and chicks will be tested for zoonotic diseases</td>
</tr>
<tr>
<td>Political conflicts of interest</td>
<td>Misconception that foreigners export Bengal</td>
<td>Medium</td>
<td>Local government and communities will be consulted and informed</td>
</tr>
<tr>
<td>Risk area</td>
<td>Present situation</td>
<td>Score</td>
<td>How risk is mitigated</td>
</tr>
<tr>
<td>---------------------------------</td>
<td>-------------------</td>
<td>-------</td>
<td>----------------------------------------------------------</td>
</tr>
<tr>
<td>Cultural conflicts of interest</td>
<td>None</td>
<td>Low</td>
<td>N/A</td>
</tr>
<tr>
<td>Floricans or breed them for food</td>
<td>about <em>ex situ</em> conservation of Bengal Florican</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 3.** Step 5: plan for harvest of eggs of *H. b. blandini.*

<table>
<thead>
<tr>
<th>Year</th>
<th>Stoung-Chikreang</th>
<th>Baray</th>
<th>Sankor</th>
<th>Bakan</th>
<th>Koup Preah Boung Trea</th>
</tr>
</thead>
<tbody>
<tr>
<td>2019</td>
<td>Only collect eggs from July onwards; monitor powerline mortality</td>
<td>Only collect eggs from July onwards; monitor field situation</td>
<td>Collect all eggs immediately; monitor field situation</td>
<td>Collect all eggs immediately; monitor field situation</td>
<td>Collect all eggs immediately; monitor field situation</td>
</tr>
<tr>
<td>2020</td>
<td>Only collect eggs from July onwards; monitor powerline mortality</td>
<td>Only collect eggs from July onwards; monitor field situation</td>
<td>Collect all eggs; monitor field situation</td>
<td>Collect all eggs; monitor field situation</td>
<td>Collect all eggs; monitor field situation</td>
</tr>
<tr>
<td>2021</td>
<td>Only collect eggs from July onwards unless powerline mortality is high, and then consider collecting eggs earlier; monitor powerline mortality</td>
<td>Monitor the situation and act accordingly</td>
<td>Monitor the situation and act accordingly</td>
<td>Monitor the situation and act accordingly</td>
<td>Monitor the situation and act accordingly</td>
</tr>
<tr>
<td>2022 onwards</td>
<td>Monitor the situation and act accordingly</td>
<td>Monitor the situation and act accordingly</td>
<td>Monitor the situation and act accordingly</td>
<td>Monitor the situation and act accordingly</td>
<td>Monitor the situation and act accordingly</td>
</tr>
</tbody>
</table>
Discussion

Conservation managers are increasingly forced into a situation where they are “held in the pressured space between extinction (as a limit on numbers and time) and the fragile wild (as a limit on intervention). Fail to intervene, and the object is lost; intervene, and the object may also be lost, although in other ways” (Reinert 2013). For many species, given the numbers of individuals available to be taken into captivity, and differences in selective pressure between captive and wild birds, it is inevitable that captive populations will soon differ from wild ones (Frankham 2008; Robert 2009) even with careful genetic management of the captive flock (Williams & Hoffman 2009; Witzenberger & Hochkirch 2011). Such changes in birds include reduced brain volume of captive-bred waterfowl compared with wild birds (Guay & Iwaniuk 2008), reduced vigilance (Carrete & Tella 2015) and inappropriate behavioral responses to predators (Griffin et al. 2000).

The first questions about captive breeding are therefore philosophical – given the genetic, morphological and behavioral changes induced by captivity, conservation managers and those who support them must be satisfied that the birds that may eventually be reintroduced to the wild are approximate allegories of the former wild populations, especially if they cannot be reintroduced back to their native range. These concepts are rarely considered explicitly in advance of ex situ conservation, but deeply-held opinions on what it means to be wild may be revealed at a stage when they can derail the process of ex situ conservation when action is most urgent. For example, effective conservation of California Condor was delayed for several years because the prevailing ideology favored a hands-off approach, until a change in
management brought all remaining individuals into captivity and eventually reversed
population declines through releases of captive-bred birds (Snyder & Snyder 2000). As another example, those running captive management of alalā (Hawaiian Crow) Corvus hawaiiensis, which is extinct in the wild, have decided to teach the crows to behave in a similar way to the original forest dwelling alalā (although their habitat is quite different since the arrival of feral pigs that sent them extinct), rather than training them to become a human commensal, as many wild populations of other crow species have done of their own volition (van Dooren 2016).

A different approach has been taken with captive-bred Asian Houbara Chlamydotis macqueenii. Captive-bred Asian Houbara have a more docile temperament and reduced migratory behavior compared to wild-bred birds (Van Heezik & Ostrowski 2001; Dolman et al. 2018). These changes lead to lower mortality in captivity but cause higher mortality among released captive-bred Asian Houbara compared to wild birds, as is also the case with captive-reared Great Bustard Otis tarda (Burnside et al. 2012; Dolman et al. 2018). Perhaps unsurprisingly, like most reintroduction attempts (Fischer & Lindenmayer 2000; Bowkett 2009) no reintroduction of bustards has been completely successful (Dolman et al. 2015; Ashbrook et al. 2016). There is a significant chance that reintroduction of H. b. blandini will also fail, even if it persists in captivity. A major impediment might be lack of habitat. If the wild population of H. b. blandini was to be extirpated, protection of the remaining fragments of grassland in the Tonle Sap floodplain may become harder, so habitat of the kind that currently associated with the species may not be available for reintroduction. While this situation is relatively common for amphibians and reptiles, which are frequently
maintained in captivity until suitable conditions exist in the wild for their release (Turtle Conservation Fund 2002; Krajick 2006; Zippel et al. 2011), it is relatively rare in birds (BirdLife International 2018a). In general, birds are harder to maintain in captivity than herptiles, but easier than mammals. Guam Kingfisher Todiramphus cinnamominus is the only bird species extinct in the wild but never likely to be returned to its native range, because the snakes which drove it extinct cannot be eradicated, although it may be introduced to a nearby island (Laws & Kesler 2012). Little Spotted Kiwi Apteryx owenii has recently been reintroduced to predator-free sanctuaries on the New Zealand mainland, prior to this it persisted for decades only in captivity and on tiny offshore islands where it had never occurred naturally (Holzapfel et al. 2008).

For these reasons, and because ex situ management is costly and risky, it can only be justified if less intrusive alternatives are unlikely to secure a species persistence (Snyder et al. 1996). By using the IUCN guidelines to assess the potential role of ex situ conservation in preventing the extinction of H. b. blandini, we were able to make a decision that comprehensively considered all of the risks, and we concluded that ex situ conservation should be attempted immediately. A similar process was used to evaluate the potential role of ex situ conservation for the South Australian subspecies of Glossy Black-cockatoo Calyptorhynchus lathami halmaturinus, which concluded that while technically feasible, captive management would be costly and the population would probably recover without it (Crowley et al. 1999). This proved correct, the population has recovered from 195 individuals in 1995 to approximately 400 individuals in 2018 without captive management (Mooney & Pedler 2005). In
contrast, we concluded that we should proceed with captive management of *H. b. blandini* and begin egg harvest in 2019 because the wild population is likely to decline at an accelerated rate owing to new threats that are impacting the only stable population, and because the chance of establishing a captive population of *H. b. blandini* is relatively high if we draw on global bustard husbandry expertise to minimize adult mortality in captivity.

Although we used the same demographic model as (Dolman et al. 2015), and our model outputs are unsurprisingly similar, the conclusions that we reached are completely different. We identify three reasons why this is the case: a. data used to parameterize the model, b. characteristics of the counterfactual ‘no ex situ’ scenario, and c. local stakeholders led the assessment process. To parametrize the *H. b. blandini* model we used data from Bengal Florican and Little Bustard when it was available in addition to the data from larger bustard species used by (Dolman et al. 2015). However, this had relatively little impact on model outputs. For instance, with egg harvest rates of 5 yr\(^{-1}\) for 5 years, probability of extinction over 50 years for Great Indian Bustard under an ‘best possible’ scenario was 17% (Dolman et al. 2015) compared with 12% for *H. b. blandini*; we interpret this as stating that there is a high chance that if *ex situ* management is done well it is likely to prevent the extinction of *H. b. blandini* and it could have done the same for Great Indian Bustard. These results are compared with a counterfactual scenario for the wild population in which no egg harvest takes place. We believe that we formulated a plausible future scenario for the wild population of *H. b. blandini*, given trends, threats and resources available for additional in situ conservation the species is likely to continue to decline to extinction.
(Mahood et al. 2019). For instance, although we believe that we know how to manage areas under rice cultivation (such as Sankor) for Bengal Florican, we do not have the resources to do this at the scale that is necessary within the time available, and success is at least partially dependent on factors outside our control, such as farmer attitudes, market forces and government policy. In contrast, the counterfactual future scenario used by (Dolman et al. 2015) imagined a situation where in situ conservation was considerably more successful than has eventuated, although what was envisaged may indeed have been possible at the time and possibly still is now. We aimed to use the IUCN guidelines (including model outputs and decision tree) to support local stakeholders to make an informed, unbiased decision about ex situ management of H. b. blandini, and having made that decision, to identify risks that needed to be mitigated to maximize chance of success.

We are determined not to let H. b. blandini join the list of taxa that could have been saved were a decision to initiate ex situ conservation taken sooner, or those such as the Bramble Cay Melomys Melomys rubicola that could have been saved were an ex situ conservation plan ever considered (Woinarski et al. 2016). Demographic modelling indicates that there is a reasonable chance, given we have taken action immediately, a captive population of H. b. blandini can be established and, in 20–30 years it should be large enough to consider reintroduction if habitat is available. We acknowledge that such a population is likely to be small and based on a limited number of founders, so failure is possible at every step. Our decision to attempt ex situ management of H. b. blandini was made based on a thorough evaluation of risks and necessary resources, informed by demographic modelling. We considered both
philosophical and practical issues fully through a decision tree. The process that we used is transparent and we hope that our tools will be helpful for others in a similar situation. We will continue to do everything possible to prevent the loss of remaining wild populations of *H. b. blandini*, but we acknowledge that if not managed properly, taking eggs from the wild may accelerate declines. We should have considered the question of *ex situ* management in 2012, when there were a number of small unprotected *H. b. blandini* populations that in hindsight had little hope for survival owing to financial and practical constraints on *in situ* conservation. Our results indicate that with support from the global community in bustard husbandry techniques, there is still a reasonable chance of establishing a captive population. However, we anticipate that *H. b. blandini* may only exist in captivity for some years, and it may never be able to be released in a situation that resembles its current wild state. We consider that this is preferable to complete loss of the taxon. We urge conservation managers faced with rapidly declining species to evaluate comprehensively the potential role of *ex situ* management, rule it out whenever there is the possibility of successful conservation of wild populations, or pursue it rapidly and with commitment where not.

**Author contributions**

SPM conceived the ideas and methodology, conducted the modelling and led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.
Acknowledgements

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Supplementary Material

Table S1. Demographic parameters for models of *Houbaropsis bengalensis blandini* captive breeding and release under four scenarios of programme quality (full range, below average, above average and best possible) and *in situ* conservation under two scenarios (current situation and future conservation), showing minimum (Min) and maximum (Max) values from which each programme iteration was sampled. Whether the parameter is restricted during the learning phase (Learn) is also shown (Y, yes; N, no; n/a: not applicable).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Scenario of captive breeding programme quality</th>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Learn</td>
<td>Full range</td>
<td>Below average</td>
<td>Above average</td>
<td>Best possible</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Learning for husbandry</td>
<td>n/a</td>
<td>2</td>
<td>4</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Proportionate adjustment of relevant parameters during learning period</td>
<td>n/a</td>
<td>0.6</td>
<td>1</td>
<td>0.6</td>
<td>0.8</td>
<td>0.8</td>
<td>1</td>
<td>0.85</td>
</tr>
<tr>
<td>Hatch rate of collected wild-laid eggs (with artificial incubation)</td>
<td>Y</td>
<td>0.5</td>
<td>0.75</td>
<td>0.5</td>
<td>0.6</td>
<td>0.55</td>
<td>0.75</td>
<td>0.6</td>
</tr>
<tr>
<td>Juvenile survival to year 1 of wild-laid captive-reared chicks</td>
<td>Y</td>
<td>0.45</td>
<td>0.85</td>
<td>0.45</td>
<td>0.7</td>
<td>0.7</td>
<td>0.85</td>
<td>0.75</td>
</tr>
<tr>
<td>Adult survival in captivity</td>
<td>Y</td>
<td>0.83</td>
<td>0.97</td>
<td>0.83</td>
<td>0.88</td>
<td>0.88</td>
<td>0.97</td>
<td>0.92</td>
</tr>
<tr>
<td>Parameter</td>
<td>Learn</td>
<td>Full range</td>
<td>Below average</td>
<td>Above average</td>
<td>Best possible</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Age of male first breeding (years)</td>
<td>N</td>
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<td>5</td>
<td>3</td>
<td>5</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Age of female sexual maturity (years)</td>
<td>N</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Learning lag (years) between first females reaching sexual maturity and breeding</td>
<td>N</td>
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<td>7</td>
<td>4</td>
<td>7</td>
<td>1</td>
<td>4</td>
<td>1</td>
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<tr>
<td>After first breeding, subsequent annual probability that adult females will breed again</td>
<td>Y</td>
<td>0.6</td>
<td>0.9</td>
<td>0.6</td>
<td>0.7</td>
<td>0.65</td>
<td>0.9</td>
<td>0.7</td>
</tr>
<tr>
<td>Clutches female(^1) yr(^{-1}), for first two years of breeding age</td>
<td>N</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Mean clutches female(^1) yr(^{-1}), for subsequent breeding</td>
<td>N</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1.3</td>
<td>1.15</td>
<td>3</td>
<td>1.3</td>
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<tr>
<td>Hatching rate of captive reared eggs (with artificial incubation)</td>
<td>Y</td>
<td>0.45</td>
<td>0.78</td>
<td>0.45</td>
<td>0.6</td>
<td>0.65</td>
<td>0.75</td>
<td>0.68</td>
</tr>
<tr>
<td>Survival of captive juvenile to 1 year old</td>
<td>Y</td>
<td>0.6</td>
<td>0.78</td>
<td>0.6</td>
<td>0.67</td>
<td>0.67</td>
<td>0.78</td>
<td>0.72</td>
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<td>Prior to first stochastic adult event: annual probability of severe adult mortality event</td>
<td>N</td>
<td>0.05</td>
<td>0.167</td>
<td>0.125</td>
<td>0.167</td>
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<td>0.167</td>
<td>0.05</td>
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<tr>
<td>Parameter</td>
<td>Learn</td>
<td>Full range</td>
<td>Below average</td>
<td>Above average</td>
<td>Best possible</td>
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<tr>
<td>First stochastic adult event: severe additive adult mortality</td>
<td>N</td>
<td>0.25 0.8</td>
<td>0.3 0.8</td>
<td>0.25 0.8</td>
<td>0.25 0.5</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Prior to first stochastic adult event: annual probability of moderate adult mortality event</td>
<td>N</td>
<td>0.2 0.5</td>
<td>0.333 0.5</td>
<td>0.2 0.5</td>
<td>0.2 0.333</td>
<td></td>
<td></td>
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<tr>
<td>First stochastic adult event: severe additive adult mortality</td>
<td>N</td>
<td>0.1 0.2</td>
<td>0.15 0.2</td>
<td>0.1 0.15</td>
<td>0.1 0.15</td>
<td></td>
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</tr>
<tr>
<td>After first stochastic adult event: annual probability of stochastic adult mortality event</td>
<td>N</td>
<td>0.2 0.5</td>
<td>0.333 0.5</td>
<td>0.333 0.5</td>
<td>0.2 0.5</td>
<td></td>
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<tr>
<td>After first stochastic adult event: additive adult mortality</td>
<td>N</td>
<td>0.1 0.2</td>
<td>0.15 0.2</td>
<td>0.1 0.15</td>
<td>0.1 0.15</td>
<td></td>
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</tr>
<tr>
<td>Annual probability of stochastic juvenile mortality</td>
<td>N</td>
<td>0.2 0.5</td>
<td>0.333 0.5</td>
<td>0.2 0.5</td>
<td>0.2 0.333</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Additive chick or juvenile mortality</td>
<td>N</td>
<td>0.08 0.15</td>
<td>0.08 0.15</td>
<td>0.08 0.15</td>
<td>0.08 0.15</td>
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<td></td>
</tr>
<tr>
<td>Annual probability of stochastic reduction in proportion of females breeding</td>
<td>N</td>
<td>0.1 0.333</td>
<td>0.25 0.333</td>
<td>0.1 0.333</td>
<td>0.1 0.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reduction in proportion of adult females breeding</td>
<td>N</td>
<td>0.15 0.2</td>
<td>0.15 0.2</td>
<td>0.15 0.2</td>
<td>0.15 0.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parameter</td>
<td>Full range</td>
<td>Below average</td>
<td>Above average</td>
<td>Best possible</td>
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<tr>
<td></td>
<td>Learn</td>
<td>Min</td>
<td>Max</td>
<td>Min</td>
<td>Max</td>
<td>Min</td>
<td>Max</td>
<td></td>
</tr>
<tr>
<td>Juvenile survival to release</td>
<td>N</td>
<td>0.45</td>
<td>0.88</td>
<td>0.45</td>
<td>0.66</td>
<td>0.58</td>
<td>0.88</td>
<td>0.75</td>
</tr>
<tr>
<td>Juvenile survival post release to 1 year</td>
<td>N</td>
<td>0.1</td>
<td>0.3</td>
<td>0.1</td>
<td>0.3</td>
<td>0.1</td>
<td>0.3</td>
<td>0.1</td>
</tr>
</tbody>
</table>

*In situ* conservation for wild and post-release

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Current situation</th>
<th>Future situation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual probability that an adult female will breed</td>
<td>n/a</td>
<td>0.33 0.8</td>
</tr>
<tr>
<td>Wild nest survival</td>
<td>n/a</td>
<td>0.4 0.7</td>
</tr>
<tr>
<td>Re-nesting rate after failure</td>
<td>n/a</td>
<td>0.1 0.5</td>
</tr>
<tr>
<td>Wild juvenile survival to 1 year</td>
<td>n/a</td>
<td>0.1 0.3</td>
</tr>
<tr>
<td>Adult survival</td>
<td>n/a</td>
<td>0.82 0.98</td>
</tr>
</tbody>
</table>
Table S2. Evidence base used to estimate *Houbaropsis bengalensis blandini*

demographic parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Evidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Learning for husbandry</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Proportionate adjustment of relevant parameters during learning period</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Hatch rate of collected wild-laid eggs (with artificial incubation)</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Juvenile survival to year 1 of wild-laid captive-reared chicks</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Adult survival in captivity</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary (One male Bengal Florican kept in captivity in Cambodia in 2018 (for the purpose of rehabilitation) survived for three months at which time it was released to the wild (ACCB unpublished data)).</td>
</tr>
<tr>
<td>Age of male first breeding (years)</td>
<td>Male Little Bustard breed at age 2 years (Bretagnolle &amp; Inchausti 2005). Captive male Houbara and McQueens Bustards breed at 1–4 years (Dolman et al. 2015).</td>
</tr>
<tr>
<td>Age of female sexual maturity (years)</td>
<td>Female Little Bustard will start breeding after 1 year (Bretagnolle &amp; Inchausti 2005). Satellite telemetry data indicate that sub-adult females (n = 2) have similar home range size to adult females (n = 7) during the breeding season (Packman 2011), so might also be breeding. Captive female Houbara and McQueens Bustards breed at 1–3 years (Dolman et al. 2015).</td>
</tr>
<tr>
<td>Learning lag (years) between first females reaching sexual maturity and breeding</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary.</td>
</tr>
<tr>
<td>Parameter</td>
<td>Evidence</td>
</tr>
<tr>
<td>--------------------------------------------------------------------------</td>
<td>--------------------------------------------------------------------------</td>
</tr>
<tr>
<td>After first breeding, subsequent annual probability that an adult females will breed again</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Clutches female⁻¹ yr⁻¹, for first two years of breeding age</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Mean clutches female⁻¹ yr⁻¹, for subsequent breeding</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Hatching rate of captive reared eggs (with artificial incubation)</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Survival of captive juvenile to 1 year old</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Prior to first stochastic adult event: annual probability of severe adult mortality event</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>First stochastic adult event: severe additive adult mortality</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Prior to first stochastic adult event: annual probability of moderate adult mortality event</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>First stochastic adult event: severe additive adult mortality</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>After first stochastic adult event: annual probability of stochastic adult mortality</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>After first stochastic adult event: additive adult mortality</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Parameter</td>
<td>Evidence</td>
</tr>
<tr>
<td>---------------------------------------------------------------------------</td>
<td>---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Annual probability of stochastic juvenile mortality</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Additive chick or juvenile mortality</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Annual probability of stochastic reduction in proportion of females breeding</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Reduction in proportion of adult females breeding</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Juvenile survival to release</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Juvenile survival post release to 1 year</td>
<td>Estimates used are same as (Dolman et al. 2015) owing to a lack of evidence to the contrary</td>
</tr>
<tr>
<td>Annual probability that an adult female will breed</td>
<td>2–6 of 6 radio tagged female Bengal Florican nested (Gray et al. 2009); 17 of 22 radio-tagged female Little Bustard nested (Lapiedra et al. 2011).</td>
</tr>
<tr>
<td>Wild nest survival</td>
<td>For n = 63 Bengal Florican nests monitored between 2008 and 2018 in a well-protected grassland survival rate was 63%, although success rates appear to be higher in recent years (WCS unpublished data). Survival rates unknown in other areas so lower estimate used by (Dolman et al. 2015) also used here; future nest survival rates assumed to be higher because birds (if still present) will be restricted to well-protected areas.</td>
</tr>
<tr>
<td>Re-nesting rate after failure</td>
<td>Satellite telemetry data and bi-model pattern of nest dates suggest Bengal Floricans can nest twice per year (Packman 2011). Rates unknown, so data from (Dolman et al. 2015) used for current situation; since evidence is equivocal on whether second nest is due to failure of the first; contra (Dolman et al. 2015) we see no reason to assert that re-nesting rates would change under future scenarios.</td>
</tr>
<tr>
<td>Wild juvenile survival to 1 year</td>
<td>No Bengal Florican data. Data from (Dolman et al. 2015) used, although with less optimistic future estimate owing to impact of power lines.</td>
</tr>
</tbody>
</table>
Parameter | Evidence
--- | ---
Adult survival | In absence of power lines, data from Cambodia indicate annual adult survival rate of Bengal Florican is 89.9% (95% CI 82.2–97.6%); this is expected to decline in the future owing to power line collisions (Mahood et al. 2016).

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Figure S1. Sensitivity of (a) mean extirpation probability and (b) geometric mean numbers of adult females, to aspects of captive-breeding performance, under the ‘best possible’ programme quality scenario substituting each parameter in turn with a value drawn from the ‘full-range’ scenario. Error bars represent 95% limits for extirpation probability and upper and lower quartiles for numbers of females in year 10; vertical dashed lines show the 95% intervals or 50% quartiles of 1,000 iterations prior to sensitivity analysis. Sensitivity to stochastic parameters was examined for the ‘best possible’ scenario, by varying the magnitude of impacts on survival or breeding by ±25%. Captive populations are established by initial harvest of 10 eggs yr⁻¹ for 5 years.
Chapter 7.

The law of small sites and its implications for conservation

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Abstract

Recent research indicates that small sites are important for conservation, but a lack of causal explanation for this counter-intuitive phenomenon hinders its general acceptance. Here, we show that a simple random-process argument, that we call the law of small sites (LSS), is sufficient to explain observed patterns of species persistence in patches. The LSS asserts that rare species will occur most often, and be found at surprising densities, in small habitat fragments. It states that this pattern is the result of multiple ecological and socio-economic processes that are distributed idiosyncratically in space and time. The LSS challenges contemporary conservation thinking and provides a theoretical and empirical foundation for the complementary role of small sites in conservation. It alters expectations about where lost species should be searched for and whether effective surrogate species exist, and it advocates for legislation and reserve design that protects small habitat patches.
Introduction

A fundamental tenet of conservation planning and practice is to prioritise the largest intact habitat patches, particularly in fragmented landscapes (Margules & Pressey 2000; Haddad et al. 2015; Fletcher et al. 2018). This axiom has been justified by multiple intersecting bodies of ecological and conservation theory. Island biogeography concludes that larger patches support more species than an equivalent area made up of small patches (MacArthur & Wilson 1967; Diamond 1975), and that the species communities in smaller patches are nested subsets of those found in the largest patches (Patterson 1987). Metapopulation theory and population viability analysis hold that demographic and colonisation dynamics will maintain a higher species richness and population abundance in large patches (Hanski & Ovaskainen 2000; Fletcher et al. 2018). Minimum viable population constraints will cause demographic extinctions in the smallest patches (Boyce 1992), in part caused by deleterious edge effects, which are stronger in small patches (Laurance et al. 2002; Haddad et al. 2015). Practically, larger habitat patches also benefit from economies of scale compared to smaller patches (Stigler 1958) and management costs per unit area are lower in large protected areas (Balmford et al. 2003). Based on these principles, systematic conservation planning prioritises the largest patches of intact habitat (Groves et al. 2003). In contrast, smaller habitat fragments are explicitly regarded as less important for conservation through the application of arbitrary size caps or use of Minimum Viable Population (MVP) size criteria (Soule & Simberloff 1986; Fahrig 2019).
In contrast, a growing body of literature asserts that small habitat patches are inordinately important for species conservation (Prugh et al. 2008; Wintle et al. 2018; Fahrig 2019). Meta-analyses indicate that the traditional metrics of island biogeography – patch size and isolation – are poor predictors of patch occupancy, particularly for rare species (Prugh et al. 2008; Fahrig 2017; Wintle et al. 2018). Moreover, while species diversity is demonstrably higher in the largest patches (Turner 1996), rare species do not typically occur in the patches with highest diversity (Prendergast et al. 1993). Put simply, rare species are often found in the smallest patches that still fulfil the ecological requirements of the species (hereafter “small sites”). This phenomenon has been observed anecdotally across a broad range of taxa and geographic locations (Fig. 1 and Table S1 in Supporting Information), which we argue is not coincidental. Understanding why small habitat patches are of high value to rare species is important for conservation (Simberloff & Abele 1982; Fletcher et al. 2018; Fahrig et al. 2019). However, no clear causal explanation for this counter-intuitive phenomenon has been proposed, so its implications remain unclear and more easily ignored.
Figure 1. Selected examples of species and habitats where small sites are disproportionately important for conservation. Selected case-studies that demonstrate the broad geographic spread of the LSS, and the diversity of taxonomic groups, life history strategies and body sizes to which it applies. Additional examples are given in the text; sources are listed in Table S1.

Here, we propose a hypothesis to explain the existence of a common but counter-intuitive small-patch phenomenon that provides a theoretical counterweight to the large-patch theories that dominate conservation discourses. Rather than focusing on the ecological role played by patch size and isolation, we propose that in the Anthropocene multiple anthropogenic processes drive the extirpation or persistence of species in habitat fragments. We call this the “law of small sites” (LSS), as it is a corollary of the “law of small numbers” (LSN). The LSN states that the unusual value of small sample objects – that is, the exceptionally high or low rates or densities often
found in small sampling units – is often a result of random processes, rather than size-related mechanisms (Tversky & Kahneman 1971). It has provided non-mechanistic explanations for phenomena as diverse as the exceptionally high rates of kidney cancer found in low-population counties in the USA (Gelman & Nolan 2017) and the outstanding standardised test results of the smallest school classes (Bourke 1986). To evaluate whether the LSS could explain the overwhelming importance of small sites for rare species, we compared patterns in a large publicly available dataset from one of the most fragmented, and most studied, biodiversity hotspots, Brazil’s Atlantic Forest (Bovendorp et al. 2017) against a simple random process model. We test the hypotheses that rare species are found most often in small patches, that they typically reach their highest density in small patches, and that this phenomenon is the result of the LSS.

**Methods**

To test the fit of the LSS to real-world data we used a publicly available dataset that contains records of 53,518 individuals of 124 species of small mammal, recorded across 283 habitat patches (Bovendorp et al. 2017). We extracted the species abundances, distributions, and patch areas from this dataset, and then re-allocated individuals randomly to habitat patches. We performed Kolmogorov-Smirnov tests on the real and random data sets to test the assumption that at the patch level, species densities in the original data set are distributed randomly among the available habitat patches. For the original and randomised data, we then calculated the local density (density of each species in each patch) relative to each species’ global density. The percentage of rare species (here defined as those that only occur in one patch,
although the results were insensitive to other definitions of rarity, such as total population less than a certain size) occurring in small patches was then calculated, where small was defined relative to the mean patch size in the fragmented landscape.

Results

Most patches in the Atlantic Forest are relatively small (Fig. 2a), indeed the area of >97% of patches is >1% the area of the largest patch. Most species are rare (for instance, more than half of species occur in less than ten patches, Fig. 2b), so it is a suitable landscape in which to test the LSS. In agreement with LSS predictions, we found that rare species commonly occur in the smaller sites (Fig. 2c). The overall pattern of rare species occupancy mirrors the overall distribution of patches (Kolmogorov-Smirnoff test, p = 0.82), as we would expect if species were lost from fragments according to multiple independent random processes. Additionally, the observed distribution of rare species’ patch sizes is indistinguishable from a random re-allocation of species occurrences to fragments, without biological, ecological or socio-economic information about the species, patches or intervening matrix (Fig. 2d). The density of each species in each site (relative to that species’ global density) in the real (Fig. 2e) and random (Fig. 2f) datasets follows the same pattern. In this dataset, the mean number of patches occupied by a species was 21.8 (range: 1–160), and mean patch size was 12,768.5 km² (range: 0.15–791,652 km²), whilst the mean patch size occupied by rare species was 4,918.1 km² (range: 2.2–47,500 km²), this difference was statistically significant (t(101) = 1.81, p = 0.03). Not only did rare species more commonly occur in small patches, they are found there at unusually high densities. For that reason, small sites are disproportionately important for rare species.
in both the empirical (Fig. 2g) and random (Fig. 2h) datasets. More than half of all rare species in the data set only occur in sites that are smaller than 3% of the mean patch area.
Figure 2. Empirical and randomized abundance patterns of small mammals in a highly fragmented biodiversity hotspot. Green bars show relative frequency distributions of (a), fragment size and (b), species abundance distributions, measured by the number of fragments they inhabit. Both data come from the Atlantic Forest case study. Relative frequency distributions of occupied fragment sizes across (c), the Atlantic Forest dataset and (d), the randomised data; white bars show sites occupied by all species; red bars show sites occupied by rare species. (e and f) Relative local density (y-axis) of each species as a function of the patch area they inhabit (x-axis) using the empirical data and the randomised data, respectively. The marker color indicates the global abundance of that species, grading from red indicating the rarest species to blue indicating the most common species. (g and h) Percentage of rare species occurring in the smallest patches (as a percent of mean patch size) in the real and randomised data respectively.

Discussion

The LSS is a conservation law of the Anthropocene, because it explains why we cannot afford to ignore small patches. We have shown that small patches are overwhelmingly more abundant in highly fragmented landscapes. In these conditions the LSS asserts that the overwhelming majority of rare species will be found in the smallest sites. Under the LSS species are extirpated from habitat patches effectively at random, and are therefore most likely to remain extant in the most numerous size class of habitat patches (i.e. the smallest). While this apparent randomness runs counter to standard ecological principles, it aligns with modern conservation beliefs (Wintle et al. 2018) and conforms to predictions that landscape-scale patterns of the
impacts of fragmentation may result from complex interactions of multiple mechanisms (Fahrig et al. 2019). Human populations impose diverse and overlapping threats to biodiversity. For most species, myriad interacting non-ecological factors – political, social, and economic – determine whether a species is lost or persists at a site (Rockström et al. 2009). These include well-documented patch-level processes that reduce species diversity and reduce the possibility of species persistence, such as edge-effects, predator-prey interactions and species dispersal (Haddad et al. 2015; Fletcher et al. 2018), as well as negative species-specific threats such as hunting and positive processes such as conservation. The unique and idiosyncratic distribution of these factors across fragmented landscapes will be familiar to any conservation practitioner. For instance, the Critically Endangered Bengal florican *Houbaropsis bengalensis*, is now most abundant in Stoung-Chikreang, one of the smallest habitat fragments in the Tonle Sap grassland, Cambodia (Mahood et al. 2019). This small site avoided detrimental agricultural changes in both breeding and non-breeding habitat (partially due to soil characteristics), secured protection from the government and NGOs, was supported by local community attitudes, and largely escaped the attention of both historical and recent hunting. For the Bengal florican to persist in a site it had to have escaped each of these existential perils successfully, since any one could have resulted in local extirpation. While each is the result of mechanistic processes, they are distributed independently in time and space (Sagarin et al. 2006). Their overall impact is multiplicative, and will therefore appear random (Scheffer et al. 2017).

The two assumptions of the LSS are satisfied by ubiquitous patterns in landscape ecology and macroecology. First, most habitat patches are small (Haddad et al. 2015),
as the size of habitat patches in fragmented landscapes consistently exhibits a power-
law distribution (Taubert et al. 2018). Second, most species are rare, exhibiting a 
lognormal distribution (McGill et al. 2007). As well as predicting that rare species 
will most often occur – and may only occur – in the smallest patches, the LSS also 
states that the rare species will occur at their highest densities in these patches. 
Persistence and high densities of species are achieved through processes that are non-
random at the patch level, but random at the landscape level where well-documented 
ecological processes are the dominant influence. High-density populations are more 
easily detected during surveys, and less vulnerable to density dependant Allee effects, 
and are therefore of high value to conservation (Courchamp et al. 2008).

The LSS does not assert that rare species will never be found in large patches, or that 
a small patch will always contain rare species. In fact, the law simultaneously states 
that while most rare species will be found in small patches, most small patches will 
contain no rare species. Many species have well-documented minimum area 
requirements, and in a fragmented landscape, there may not be any patches that are 
large enough to support species that require large areas. We therefore expect to see 
the greatest deviations from the LSS in ecological communities where rare species 
have consistently large area requirements. In any patchy landscape, the relaxation of 
extinction debts will eventually lead to loss of species from smaller patches 
(Kuussaari et al. 2009; Haddad et al. 2015), so the LSS does not indicate that there 
will always be a patch within each landscape where each species can persist. The LSS 
is only relevant to the impacts of habitat fragmentation, not to the reduction in habitat 
area that often accompanies it (Fahrig 2017). It does not make any claims about the
relationship between patch size and species diversity, we agree that large areas of habitat support more species than small areas of habitat (Turner 1996; Haddad et al. 2015).

The LSS has implications for species monitoring, conservation planning and policy. The LSS suggests that searches for lost species should target small patches (above a biologically-relevant threshold size) rather than the largest patches of habitat. The periphery of species ranges are typically patchier and exhibit more spatially variable densities than the core (Channell & Lomolino 2000), therefore it is little surprise that most mammal rediscoveries have been made in small, sub-optimal patches in the periphery of the species historical range (Fisher 2011). The LSS implies that it is one of the smallest biologically-relevant patches that is most likely to support a population of a given lost species, and that it is at such locations that a lost species is most likely to occur at a high density (and therefore be more easily detected). We therefore recommend that searches for lost species such as Edwards’s Pheasant *Lophura edwardsi* should counter-intuitively avoid wasting valuable time and effort surveying the largest patches within a species historical range, and instead identify, prioritise and rapidly survey small patches in the periphery of the species range, even if they contain suboptimal habitat.

As a consequence of the bias towards survey of large intact habitat patches, many small patches in need of protection to conserve specific rare species have not been prioritised or even identified (Fahrig et al. 2019). Moreover, the LSS asserts that the most significant populations of the rarer species will be in small patches. This runs
counter to nestedness theory, which underpins conservation planning, and assumes that large, intact areas of habitat will support all of the species in a landscape, including those of greatest conservation concern (Patterson 1987). However, patch area is a poor predictor of occupancy (Prugh et al. 2008), small sites are known to be disproportionately important for ensuring that all species are conserved (Armsworth et al. 2018) and there is no empirical evidence that a group of small patches has lower ecological value than a large patch of the same area (Fahrig 2017). Although protection of large intact ecological systems is crucial to conserve the highest diversity areas and preserve ecosystem function and ecosystem services (Watson et al. 2016), the LSS gives reason to the argument for the complementary role played by small sites in safeguarding rare species where comprehensive conservation plans should include sites of all sizes.

The distribution of most species is incompletely known despite centuries of species survey (Pimm 2000). The solution has been to use the distribution and abundance of common, easily detected surrogate species to ensure that rarer species that are hard to detect will also be protected (Margules & Pressey 2000). The LSS explains why surrogate species are frequently ineffective (Andelman & Fagan 2000; Rodrigues & Brooks 2007). It states that umbrella species typically occur at densities close to the global mean regardless of patch size, whilst rare species are likely to be at higher densities in small patches.

The LSS also means that a patch that supports a high density of one rare species is unlikely to support a high density of another. It might also be assumed that sites
support a high population of a rare species possess conditions that are favorable to rare species in general. The LSS implies that even when species have similar habitat requirements and face similar threats, the processes that determine persistence for each species will remain effectively random. Thus a patch that supports a high density of any one rare species is unlikely to support a high density of another rare species. This phenomenon can be illustrated by the modern distribution of sympatric Critically Endangered primates in northern Vietnam, each species occurs at a high density in just one patch, whilst they are absent from all other remaining patches (IUCN 2019).

Inconveniently for conservation planners, the LSS indicates that surrogate species will work no more frequently than would be expected by chance regardless of whether they are common or rare.

The LSS has equally inconvenient implications for policy. Under typical legislative frameworks, all habitat patches below a threshold size are thought likely to be of low conservation value, and can often be cleared without assessment (Fahrig et al. 2019). However, the LSS states that the most important sites for rare species – and therefore those that are most in need of protection – are likely to be small sites. Legislation should therefore mandate survey of all small habitat patches prior to clearing, even though most will be of no value for rare species (Tulloch et al. 2016). It is logistically and financially easier to arrange the conservation of smaller patches, which means that when important small patches are found they can at least be protected rapidly (McCrea-Strub et al. 2011).
The LSS will most commonly apply in the most fragmented landscapes, which are often the hotspots of biodiversity and the areas of greatest importance to the prevention of extinction. Already more than 70% of the world’s forest is within 1km of an anthropogenic edge (Haddad et al. 2015), and habitat fragmentation is predicted to increase in the coming decades (Taubert et al. 2018), further skewing the distribution of habitat patches and increasing the relevance of the implications of the LSS. Rare species are likely to occur at extreme densities in small patches because of the LSS, with direct and important implications for conservation planning and practice. Our conclusions complement rather than compete with the orthodox conservation approach of focusing on large patches and intact landscapes. We do not necessarily advocate prioritising the protection of small patches over large ones, and we definitely do not advocate the division of large patches into multiple small patches. Although the importance of small patches for conservation is well known (Wintle et al. 2018; Fahrig 2019), the LSS provides an explanation for their importance, so they can no longer be ignored in efforts aimed at preventing extinctions.

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**Supplementary Material**

**Supplementary Table S1.** Sources used in production of Fig. 1

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Chapter 8. Conclusion

8.1 Introduction

Bustards have been a feature of the grasslands of tropical Asia for millions of years. The floricans evolved there. Much later humans evolved and colonized Asia where they decimated populations of large mammals that maintained grasslands, and eventually began to cultivate crops in the floodplains of rivers. The Bengal Florican was able to adapt to these gradually changing circumstances and persist in the modified landscape, but its population has crashed in modern times as Cambodia has undergone rapid development and change.

The conservation literature is littered with predictions of species extinctions. However unpalatable these are, they are consistent with global trends (Dirzo et al. 2014; Pimm et al. 2014; Ceballos et al. 2015). I make a similar prediction in Chapter 3 regarding *H. b. blandini* when I state that it might be extinct within five years based on the size of the population and the rate of decline. The IUCN Red List implies a probability of extinction of at least 50% within 10 years or 3 generations (whichever is longer) for species that qualify as Critically Endangered (IUCN 2019). However, fewer species have gone extinct than would have been expected since 1994, when the first status assessment of birds was made (Brooke et al. 2008). Conservation of small populations of highly threatened species has prevented extinctions, and in some cases even allowed populations to increase (Butchart et al. 2006). Although it is declining
overall, the Bengal Florican population is stable at Stoung-Chikreang BFCA, which is
the only site to have received significant conservation attention. Evidently it is
possible to protect a population in a Cambodian context, so there is hope that H. b.
blandini can defy the Red List odds.

8.1.1 Threats are intensifying

Although there is evidence that conservation has had a local impact on the status of H.
b. blandini, the threat assessment in Chapter 4, rate of habitat change due to
agricultural intensification described in Chapter 5, and impacts of the power lines that
are evaluated in Annex 1, indicate that all sites that support H. b. blandini face threats
that may be intractable to prevent and to which it may succumb in the time that is
available given the rate of decline. Since (Mahood et al. 2016) was published, there is
still no effective way of marking power lines to prevent (or even significantly reduce)
bustard collisions (Bernardino et al. 2018), and the line markers that Electricité du
Cambodge committed to installing where the power line crossed Stoung-Chikreang
BFCA have never been installed (S. Mahood pers. obs.). It has recently been shown
that marking power lines with UV lights can reduce crane mortality on power lines by
98% (Dwyer et al. 2019), testing this method in areas with bustards is a priority.

In Chapter 3, I speculate that Allee effects may doom sub-populations of Bengal
Florican when the amount of suitable habitat at a given site drops below 25 km² and
hasten extinction overall. Below that threshold there is insufficient habitat to support a
functioning lek, so displaying male Bengal Floricans abandon the site. Recent
research into breeding systems of Little Bustard highlights another possible Allee effect that acts on bustard populations: males select lek sites based on the presence of females (Devoucoux et al. 2019), so if there are very few females remaining in a population (as in Cambodia) then there may be a reduced chance that bustards find suitable grassland remnants. Yet another additional cause for concern is that Cambodia’s Bengal Florican population might be ageing if productivity has been low for more than a decade, the sperm of older bustards retards chick development, which could lower productivity further (Preston et al. 2015).

8.2 Research limitations and directions for future research

My research focused on evaluating the impacts of Bengal Florican conservation to date, and planning the next steps. As conservation managers begin to implement the measures discussed in Chapters 4 and 5, there is a need to complement the annual Bengal Florican monitoring with vegetation and invertebrate monitoring. Long-term plots should be established in protected areas, and agricultural areas where conservation managers are working with farmers to promote low intensity agriculture, to assess the impacts of conservation interventions. Although the Bengal Florican population will always be the ultimate measure of success, the monitoring method is not able detect subtle changes in population. In this context it is also important to begin to monitor change in the status of Bengal Florican habitat and food requirements, which are likely to respond more quickly to changes in management.
My research into habitat trends was restricted to the Tonle Sap Floodplain, where the Bengal Florican breeds. Habitat requirements of Bengal Floricans in the non-breeding season are fairly well known, but habitat trends are poorly known and there is a need to evaluate the status of their preferred habitat. Like other bustards, Bengal Floricans roam extensively during the non-breeding season (Packman 2011), so conservation managers have begun to promote low intensity agriculture, especially legumes, in areas that Bengal Floricans use. There is a need to monitor vegetation structure and insect biomass in these fields, to test whether conservation interventions are creating suitable habitat for Bengal Floricans.

Although it is not of direct relevance to conservation managers, there is also a need to re-evaluate the taxonomic status of the two Bengal Florican taxa. My own field observations, interactions with Indian and Nepali conservationists during my research, and reading the type description of *H. b. blandini* for the first time while researching for my literature review, have made me increasingly convinced that the two taxa differ in aspects of their courtship displays and in the shape and location of the display plumes. These differences need to be quantified, and samples taken to permit genetic analysis, in order to assess the distinctiveness of the taxa. Species are the taxonomic unit at which conservation priorities are typically set, so it is of more than just empirical interest that this is investigated. Nevertheless, whether *H. b. blandini* is distinct at the species level or not, rapid conservation action rather than additional research is the priority.
8.3 Defining success

Organisations such as the Ministry of Environment and Wildlife Conservation Society (WCS) that have taken on the task of preventing the extinction of Bengal Florican in Cambodia face an ever-increasing list of threats that they must address if they are to prevent its extinction. In this context it is critical to define what success would look like for the conservation of H. b. blandini to enable conservation practitioners to prioritize actions and feel some degree of satisfaction when small victories are achieved. Highlighting achievements, however small, is critical for maintaining the morale and commitment of individuals and organizations involved in conservation (Garnett & Lindenmayer 2011). In the case of H. b. blandini, it seems implausible that the taxon could ever be restored to historical levels of either population or distribution, even if the late 1990’s was taken as the reference point. At least in the short term, success might take three forms, which are hopefully complementary. These are: protection of at least one sub-population in the wild, preservation of the taxon in captivity, and the avoidance of extinction of bustards in South Asia through better coordination.

8.3.1 Protect at least one sub-population in the wild

The first priority and measure of success should be to maintain at least one sub-population of H. b. blandini in the wild. Contrary to much of the literature on reserve design and impacts of habitat fragmentation (Margules & Pressey 2000; Laurance et al. 2011), this does not need to be at a large site. The importance of small sites for conservation is increasingly recognized (Wintle et al. 2018) and, as explained in Chapter 7 there are reasons to suggest that a small site might actually be the most
successful place to protect Bengal Florican in the wild, provided it is large enough to
support a breeding lek. Small sites are inherently vulnerable to threats, for instance, a
small grassland reserve can be entirely destroyed by a few people with tractors in one
night, but the same reserve could be patrolled in its entirety every night. If the impacts
of power lines at Stoung-Chikreang BFCA cannot be mitigated, then the only other
small site available for the subspecies is Baray BFCA. That site could support a
population of more than one hundred displaying male Bengal Florican, based on
extrapolations of densities at Stoung-Chikreang BFCA. This number may be
insufficient to prevent inbreeding, and would be vulnerable to other Allee effects.
Nonetheless it may be the best that can be achieved under the circumstances. Other
Bengal Florican populations need not be ignored, indeed attempts are underway at all
sites that still support *H. b. blandini* either to protect them or take the birds and/or
their eggs for captive breeding (see below). If it sounds defeatist to hope for just one,
small, well-protected area of grassland or low intensity agriculture in which a
population of Bengal Florican can persist then it should be remembered that this is
little different to what has been planned for the reintroduction of Great Bustard to the
UK (Osborne 2005).

If the aim is to preserve one site with a population of *H. b. blandini* then the critical
question is how. This will need to be the subject of stakeholder consultation,
potentially in the form of revision of the Bengal Florican National Action Plan, but
here I outline two initial suggestions. First, the boundaries of Baray BFCA should be
reviewed and the large Chinese irrigated rice concession that takes up 25% of the
protected area excised. At the same time, Chong-Duong BFCA, which is located
immediately to the north of Baray BFCA should be de-gazetted because it has not supported a single displaying Bengal Florican since 2009. Removing these areas of industrial agriculture from the protected area network should be sufficient to gain the political support needed to extend Baray BFCA to encompass the unprotected grassland to the south-east (this area was previously part of the protected area network when Baray was an IFBA), which supports an important lek of Bengal Florican (ideally the protected area should also be extended to incorporate some of the scrub to the south and west, because this area supports the only remaining breeding population of the Critically Endangered White-shouldered Ibis *Pseudibis davisoni* in the Tonle Sap Floodplain (Wright et al. 2013)).

At the same time as revising the boundaries of the protected area, there is a need to reduce threats to the Bengal Florican population at Baray BFCA where as I show in Chapter 4, the population is subject to opportunistic hunting and encroachment. It has been theorized that economic and social development might lead to reduced threats to species (Sanderson et al. 2018), however, these changes will not come quickly enough for Bengal Florican. In time there is likely to be a reduction in the number of rural people working in the fields as people migrate to the cities, leading to a reduction in opportunistic hunting of Bengal Florican for subsistence purposes. In Chapters 3 and 4 we discuss how this threat has apparently been reduced at Stoung-Chikreang BFCA through a behavior change campaign and a long period of social engagement to a point where it is not causing the population to decline. This needs to be replicated at Baray BFCA. Ongoing economic development is likely to lead to an increase in the scale and severity of agricultural intensification, which will put greater pressure on
the remaining areas of grassland and low intensity agriculture in and adjacent to Baray BFCA. In Chapter 5 I suggest that a case could be built for better protection of seasonally flooded habitats in the Tonle Sap Floodplain, not only for the conservation of Bengal Florican, but also for the ecosystem services that these habitats provide to communities. Communicating this information clearly to decision makers in government and development agencies (who typically provide financing for irrigation infrastructure improvements that facilitate agricultural intensification) is essential. Equally important is to help the communities that gain benefits from extensive agricultural systems (such as high fish catches), to manage those habitats and protect them in collaboration with relevant government agencies. For a small breeding-range protected area to maintain a wild population of Bengal Florican effectively there must also be sensitive management of agricultural areas used by Bengal Floricans during the non-breeding season, when they range too widely to stay within the bounds of a small protected area. This will by necessity take the form of some kind of agri-environment scheme implemented in collaboration with farmers and the private sector. One potential option for this, involving the Sustainable Rice Platform, is discussed in Chapter 4, but these measures will need to be scaled up rapidly.

8.3.2 Establish a captive insurance population

Success in *H. b. blandini* conservation will also require a captive population to be established. The risk of extinction of the wild population is too great to avoid the issue. As described in Chapter 6, the captive population will likely be formed from a small founder population, and may become rapidly adapted to captivity (Dolman et al. 2018), if a captive population can be formed at all. With hindsight, the notion of
captive breeding should have been raised 5–10 years ago when there were several tiny *H. b. blandini* populations that, for reasons of cost, were never likely to receive any conservation attention and have indeed not survived without it. Even if captive management is successful, there is very little possibility that there will be enough captive Bengal Floricans to begin releasing birds until 2050 at the earliest. Within that time period, *H. b. blandini* will either be extinct in the wild, or there will be a successful *in situ* conservation program. Releasing captive-bred Bengal Floricans that have been subject to generations of genetic and behavioral changes into that population would be unwise. Instead, the role of a captive *H. b. blandini* population is to guard against the risk of extinction of the taxon in case *in situ* conservation fails, and when sufficient birds exist in captivity, to establish a new *in situ* population elsewhere.

It is impossible to predict what Cambodia will be like in 2050, but based on global economic, social and demographic trends, most people will probably live in cities, most land will either be in relatively well-managed protected areas or under intensive agriculture, and there may be a growing interest in nature conservation (Sanderson et al. 2018). Under these conditions a population of Bengal Florican, which will likely have lost their urge to migrate and may be naïve towards people and predators (Griffin et al. 2000), could be established in a small nature reserve near one of the cities on the periphery of the floodplain of the Tonle Sap Lake (which will probably have lost its unpredictability owing to hydropower development on the Mekong (Pokhrel et al. 2018)). This version of wild may be unpalatable to some conservationists (Stokes 2018), but numerous island taxa are maintained in the wild
only at small sites from which they cannot disperse and at which they must be provided with supplementary food, such as the Kakapo *Strigops habroptilus* in New Zealand, and Pink Pigeon *Nesoenas mayeri* in Mauritius (Jones & Merton 2012). Almost all ecosystems are to an extent human-modified (even the most remote parts of the Arctic are impacted by human-induced climate-change) and species now exist along a continuum of wildness such that the lines between captive and wild are increasingly blurred (Redford et al. 2012). Habitats and ecosystems will change, but what matters is that we preserve as much of the genetic diversity of life as possible by preventing the extinctions of species. “Island style” intensive management is rarely used for conservation of continental bird species, but it has been prevalent in conservation of some continental large mammals for many years. For instance, Southern White Rhinoceros *Ceratotherium simum* was reduced to fewer than 20–50 individuals at the end of the nineteenth century, but, following a program of captive management, it now numbers at least 20,000 individuals in strictly protected, fenced reserves to which they have been reintroduced (or introduced), with the entire population managed to maximize genetic diversity through translocations (Amin et al. 2006; IUCN 2019). Such strategies are likely to be necessary for *H. b. bengalensis* and it may be increasingly necessary for other continental bird taxa.

8.3.3 Improve collaboration between bustard conservationists

Very few continental bird taxa have gone extinct in modern times (Szabo et al. 2012), but all of the tropical Asian bustard taxa are at a very high risk of global extinction (Collar et al. 2017). A third measure of the success of *H. b. blandini* conservation is whether it can help to prevent the extinction of other bustard taxa through sharing of
knowledge and experience. Although in situ bustard conservation in Cambodia might ultimately fail, some of the conservation activities in low intensity agricultural areas might succeed in a different political or social context and could be relevant for bustard conservation in India and Nepal. There is an urgent need to address threats to bustards outside of protected areas in South Asia, particularly for Lesser Florican because it no longer breeds in protected areas, but also for Bengal Florican in the non-breeding season (Dutta et al. 2013; Dutta et al. 2018). In Chapter 4 I have developed a framework for collaboration between Bengal Florican conservationists that could be used to guide this process, and there are plans to build on this to include other bustard taxa. The metrics can be used to measure progress and document successes, whilst the framework can be used to hold conservationists to account to ensure that plans lead to action.

8.4 Conclusion

Cambodia is undergoing rapid change and the population of H. b. blandini is declining rapidly as a result. The remaining population is tiny and the situation is urgent. Conservationists must adapt quickly to changing circumstances and new opportunities, adapting tools from elsewhere and not fearing failure. Preventing the extinction of H. b. blandini will require collaborative effort from government, NGOs, civil society and the private sector to implement rapidly a suite of conservation measures even though each has a low probability of success. However, the alternative is certain loss of one of the most charismatic birds in south-east Asia. While a little luck will be essential, luck usually comes only to those who are trying.
8.5 References


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Appendix 1.

Proposed power transmission lines in Cambodia constitute a significant new threat to the largest population of the Critically Endangered Bengal Florican *Houbaropsis bengalensis*
Proposed power transmission lines in Cambodia constitute a significant new threat to the largest population of the Critically Endangered Bengal florican *Houbaropsis bengalensis*

**SIMON P. MAHOOd, JOÃO P. SILVA, PAUL M. DOLMAN and ROBERT J. BURNSIDE**

**Abstract** The remaining Indochina population of the Critically Endangered Bengal florican *Houbaropsis bengalensis* breeds in the floodplain of Cambodia’s Tonle Sap Lake. The population has declined substantially but survival rates have not been published previously. Survival could potentially be reduced by the planned construction of high-tension power transmission lines that may begin in 2016. Using data from 17 individuals monitored by satellite transmitters over 4 years we estimated the annual adult survival rate to be 89.9% (95% CI 82.2–97.6%), which is comparable to that of other bustards. Interrogation of movement paths revealed that for the 13 individuals for which we had sufficient data for non-breeding seasons, all annual migration routes between breeding and non-breeding areas crossed the proposed route of the transmission line. The route also impinged on the margins of one important and one minor breeding concentration. A review of bustard collision rates confirmed the vulnerability of bustards to power lines, and the proposed development therefore presents an additional threat to the future of this species in Indochina.

**Keywords** Bengal florican, bustard, Cambodia, collision mortality, *Houbaropsis bengalensis*, power line, Tonle Sap

**Introduction**

Rapid economic growth drives increasing energy demands (Toman & Jemelkova, 2003). In South-east Asia this demand is being met through the development of hydropower dams on the Mekong River and its tributaries (MRC, 2011), with the inevitable construction of associated high-voltage power transmission lines. Power lines are a well-documented threat to birds globally (e.g. Jenkins et al., 2016), with hundreds of millions of birds killed annually through collisions and, to a lesser extent, electrocution (e.g. Rioux et al., 2013; Loss et al., 2014). Collisions have a disproportionate impact on species with high wing-loading and low aspect, whose heavy bodies and small wings restrict rapid reactions to obstacles (Bevanger, 1998), and species with narrow fields of view in the frontal plane, such as storks, cranes and, in particular, bustards (Martin & Shaw, 2010).

The Critically Endangered Bengal florican *Houbaropsis bengalensis* occurs in South-east Asia and the Indian sub-continent; *H. bengalensis blandini* is the only bustard taxon in South-east Asia, where it is now restricted to the Tonle Sap floodplain, in Cambodia (Collar et al., 2014). The population declined by an estimated 44–64% between 2005–2007 and 2012, when only 216 (95% CI 156–275) displaying males remained (Packman et al., 2014), primarily as a result of rapid loss of floodplain grassland (Packman et al., 2013). The effects of other potential threats, such as hunting and nest predation by domestic dogs, are unknown. Population trends at Cambodian breeding sites vary, although most are negative (Packman et al., 2014); the only stable population is in Stoung–Chikraeng Bengal Florican Conservation Area (WCS Cambodia, unpubl. data, 2016). Bengal floricans disperse annually from their breeding grounds as lake levels rise (Gray, 2008; Packman, 2011), migrating up to 60 km to degraded Dipterocarp forest and farmland (Packman, 2011). Outside South-east Asia the nominate subspecies is restricted to an estimated 75–96 individuals in Nepal and fewer than 100 in India (BirdLife International, 2016).

Basic demographic parameters, which are important in the diagnosis of population declines, are poorly known for the Bengal florican. Breeding productivity is unquantified; however, a preliminary estimate based on a limited data set indicated potentially high adult survival (Packman, 2011), as is typical for many bustard species (Dolman et al., 2015). The planned construction of a power line adjacent to the major breeding concentrations of the Bengal florican could potentially intercept migration routes between these and non-breeding areas, and could pose a serious threat to this species.

In contrast to most other countries in South-east Asia, Cambodia has a relatively low human population density...
and is still ranked as a Least Developed Country (UN- 
OHRLLS, 2015), with only c. 250 km of power transmission 
lines (ADB, 2013). This is set to change over the next few 
years following the announcement in 2015 of plans for 230 
kV power transmission lines running from Battambang to 
Siem Reap and along the northern edge of the Tonle 
Sap floodplain (Fig. 1a) through Kampong Thom and 
Kampong Cham (350 km; hereafter Tonle Sap power line), 
linking that line at Kampong Thom with the international 
border with Laos PDR (190 km) and linking Kampong 
Cham with the Lower Sesan 2 hydropower dam in Stung 
Treng Province (125 km) (Electricité du Cambodge, 
2015a,b; The Cambodia Daily, 2015). The breeding grounds 
of 81% of the Cambodian Bengal florican population are 
located in the floodplain immediately to the south or along the 
route of the proposed Tonle Sap power transmission line 
(Packman et al., 2014; Fig. 1a). In common with most coun-
tries Cambodian government policy and practice prioritizes 
short-term economic development. Pre-Environmental Impact 
Assessments (EIA) were conducted for the proposed 
Tonle Sap and Kampong Thom–Lao PDR power transmis-
sion lines (possibly in advance of a full EIA) and were ob-
tained by the authors after submission of the manuscript. 

We provide a baseline estimate of annual survival rates of 
Cambodia’s Bengal floricans prior to the construction of 
power transmission lines. To assess qualitatively the poten-
tial impact of power lines on the Bengal florican we reviewed 
published and unpublished data on rates of collision be-
tween bustards and power lines and examined the location of 
breeding and non-breeding areas and migration routes in 
relation to planned transmission routes.

Methods

Mortality rate in the absence of power lines

During May 2010–January 2015 11 male (10 adults, 1 sub-
adult) and six female (5 adults, 1 subadult) Bengal floricans 
were monitored using Argos platform telemetry transmit-
ters (35 g Solar Argos PTT-100 and 45 g Solar Argos/GPS 
PTT-100 45 g. Microwave Telemetry, Inc., Columbia, 
USA; 30 g, North Star Science and Technology, King 
George, USA; Table 1). This sample represented c. 4% of 
the 2012 adult population of Bengal floricans in Cambodia 
(assuming an approximate 1:1 sex ratio). All transmitters 
had an expected transmission lifespan of c. 3 years as stated 
on their product sheets (Microwave Telemetry, Inc., 2015; 
North Star Science and Technology, 2015) and remained 
charged using solar power, except for one non-solar unit 
with a 1-year life expectancy. Catch methods are described 
in Packman (2011). The transmitters were attached using 
permanent Teflon backpack harnesses with no possibility of 
tag loss, and unit failure was considered to be unlikely. 

As mortalities could not be interpreted in the field, out-
comes were interpreted from engineering data about the ac-
tivity state of the transmitter, including Argos location 
classes 2 (1 SD of estimated error: 250–500 m) and 3 (1 SD 
of estimated error: < 250 m), and temperature, activity sen-
or and voltage data (following Burnside et al., 2016). Spatial 
error in Argos fixes meant that location data alone could not 
confirm mortality (with uncertainty as to whether a position 
was static), but location data could confirm that an individ-
ual was still alive when seasonal movements exceeded the 
error margin of location fixes. Mortality was inferred 
when the activity sensor remained static, the mean unit tem-
perature dropped and the voltage pattern changed from the 
previous cycle (although the unit typically initially con-
tinues to transmit). Sudden cessation of transmission 
where engineering data had been regular with no indication 
of voltage deterioration was also attributed to death and 
subsequent destruction, burying or permanent covering of 
the solar panel leading to permanent signal loss (Burnside et al., 2016). In contrast, progressive deterioration of the 
voltage and increasing gaps in transmission of engineering 
data are signs of transmitter failure. Consequently, the fate 
of all individuals was known (1 = death and 0 = unit failure 
or still alive at the end of the data transmission period), fa-
cilitating direct measures of daily mortality rate, with vari-
ance estimated by binomial error using the number of 
exposure days as the number of binomial trials, with the an-
nual survival estimated to be (1 − daily mortality rate)365.

Assessment of risk from the proposed power lines

We collated and reviewed quantified estimates of bustard 
mortality rates from power line collisions, based on pub-
lished studies located using Web of Science, and unpub-
lished reports that were known to us. To the best of our 
knowledge only studies in which repeat surveys were con-
ducted on cleared lines were included in our review. 

Bengal florican breeding and non-breeding areas were 
located and mapped based on 10 years of field surveys 
(Davidson, 2004; Gray et al., 2009; Mahood et al., 2013) 
and unpublished satellite transmitter data (this study). 
Movement paths were interpreted from platform telemetry 
transmitter relocations, filtered using only locations of class 
2 or 3. Any locations outside Cambodia were excluded as 
outliers. To quantify the risk of encountering power lines 
during annual movements between breeding and non-
breeding areas, movement paths were examined and the 
occurrence and date of each potential power line crossing 
event was recorded.
Results

Survival rate in the absence of power lines

The rates at which transmitters provided high-quality location fixes (i.e. classes 2 or 3) varied between individuals (total = 12,782 filtered locations; Table 1). A greater frequency of engineering data was received (118,700 lines; Table 1), with fewer gaps (54.6% of exposure days covered), and thus outcomes could be determined for all monitored individuals. The 17 individuals were monitored for a total of 20,566 exposure days between 2010 and the end of January 2015. Three evident mortalities interpreted from engineering data together with three sudden cessations with no prior transmitter failure or battery deterioration (Table 1) indicated a total of six mortalities (one female, five male) during the study. One non-solar powered unit reached its 1 year life-expectancy (Table 1). The other 10 individuals survived and were transmitting until the end of the programme. Annual survival was estimated to be 89.9% (95% CI 82.2–97.6%).

Assessment of risk from the proposed power lines

Published and unpublished data for five bustard species across 11 studies and five countries (Table 2) confirmed...
Table 1 Deployment and outcomes for 17 Bengal floricans *Houbaropsis bengalensis* tracked via Argos satellite transmitters between May 2010 and February 2015. Argos no. refers to the number of Argos location fixes of quality class 2 or 3. Engineering no. refers to the number of engineering transmissions received containing information on activity, temperature and voltage sensors, from which outcomes can be inferred. Engineering days refers to the number of days during the monitoring period on which engineering data were received. Exposure days refers to the total number of days an individual was monitored alive, as inferred from the Argos and engineering data. Outcomes are self-explanatory (except for EOP: individual alive at end of programme), and coded as 1 = dead, 0 = alive on last monitoring day.

<table>
<thead>
<tr>
<th>Tag ID</th>
<th>Sex</th>
<th>Deployed</th>
<th>1st location date</th>
<th>Last location date</th>
<th>Argos No.</th>
<th>Days</th>
<th>Last date engineering received</th>
<th>Exposure days</th>
<th>Outcome</th>
<th>Mortality</th>
</tr>
</thead>
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<tr>
<td>72047</td>
<td>M</td>
<td>Mar. 2008</td>
<td>23 May 2010</td>
<td>565</td>
<td>30 Jan. 2015</td>
<td>1,350</td>
<td>772</td>
<td>1,715</td>
<td>EOP (0)</td>
<td>12.594°N 104.86°E</td>
</tr>
<tr>
<td>28410</td>
<td>F</td>
<td>Feb. 2009</td>
<td>30 May 2010</td>
<td>146</td>
<td>3 June 2012</td>
<td>247</td>
<td>140</td>
<td>758</td>
<td>Death (1)</td>
<td>12.755°N 104.676°E</td>
</tr>
<tr>
<td>90587</td>
<td>F</td>
<td>Feb. 2009</td>
<td>18 May 2010</td>
<td>1,591</td>
<td>1 Feb. 2015</td>
<td>15,845</td>
<td>1,302</td>
<td>1,720</td>
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<td>12.594°N 104.86°E</td>
</tr>
<tr>
<td>90591</td>
<td>M</td>
<td>Mar. 2009</td>
<td>23 May 2010</td>
<td>14</td>
<td>15 June 2010</td>
<td>141</td>
<td>15</td>
<td>32</td>
<td>End of battery (0)</td>
<td>12.266°N 104.992°E</td>
</tr>
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<td>52015</td>
<td>F</td>
<td>Feb. 2010</td>
<td>28 May 2010</td>
<td>677</td>
<td>31 Jan. 2015</td>
<td>7,432</td>
<td>723</td>
<td>1,709</td>
<td>EOP (0)</td>
<td>12.594°N 104.86°E</td>
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<td>20 May 2010</td>
<td>751</td>
<td>31 Jan. 2015</td>
<td>8,071</td>
<td>767</td>
<td>1,718</td>
<td>EOP (0)</td>
<td>12.231°N 105.174°E</td>
</tr>
<tr>
<td>52123</td>
<td>M</td>
<td>Feb. 2010</td>
<td>22 May 2010</td>
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<td>1 Feb. 2015</td>
<td>16,645</td>
<td>1,083</td>
<td>1,716</td>
<td>EOP (0)</td>
<td>12.231°N 105.174°E</td>
</tr>
<tr>
<td>52129</td>
<td>F</td>
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<td>18 May 2010</td>
<td>468</td>
<td>1 Feb. 2015</td>
<td>14,776</td>
<td>1,190</td>
<td>1,721</td>
<td>EOP (0)</td>
<td>12.231°N 105.174°E</td>
</tr>
<tr>
<td>52132</td>
<td>F</td>
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<td>20 May 2010</td>
<td>2,430</td>
<td>1 Feb. 2015</td>
<td>18,687</td>
<td>1,326</td>
<td>1,718</td>
<td>EOP (0)</td>
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<td>1,718</td>
<td>EOP (0)</td>
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</tr>
<tr>
<td>Species</td>
<td>Location</td>
<td>Line type</td>
<td>Survey effort (km)</td>
<td>Study duration (months)</td>
<td>Visit interval (days)</td>
<td>No. of collisions</td>
<td>Collision rate (km(^{-1}) yr(^{-1}))</td>
<td>Source</td>
<td></td>
<td></td>
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<td>-----------------------------</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Great bustard <em>Otis tarda</em></td>
<td>Cáceres, Spain</td>
<td>T</td>
<td>3.9</td>
<td>24</td>
<td>30–60</td>
<td>23</td>
<td>2.95</td>
<td>Janss &amp; Ferrer (1998)</td>
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<td></td>
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<tr>
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<td>Rosalejo, Spain</td>
<td>T</td>
<td>10</td>
<td>12</td>
<td>15</td>
<td>1</td>
<td>0.10</td>
<td>Alonso &amp; Alonso (1999)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Little bustard</td>
<td>Rosalejo, Spain</td>
<td>T</td>
<td>10</td>
<td>12</td>
<td>15</td>
<td>12</td>
<td>1.20</td>
<td>Alonso &amp; Alonso (1999)</td>
<td></td>
<td></td>
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<tr>
<td>Great bustard</td>
<td>Almaraz, Spain</td>
<td>T</td>
<td>10</td>
<td>12</td>
<td>15</td>
<td>2</td>
<td>0.20</td>
<td>Alonso &amp; Alonso (1999)</td>
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<td>Usagre, Spain</td>
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<td>0.10</td>
<td>Alonso &amp; Alonso (1999)</td>
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<td></td>
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<tr>
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<td>T</td>
<td>10</td>
<td>12</td>
<td>15</td>
<td>2</td>
<td>0.20</td>
<td>Alonso &amp; Alonso (1999)</td>
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<td></td>
</tr>
<tr>
<td>Little bustard</td>
<td>Rosalejo, Spain</td>
<td>T</td>
<td>10</td>
<td>12</td>
<td>15</td>
<td>23</td>
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<td>Neves et al. (2005)</td>
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<tr>
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<td>T</td>
<td>48</td>
<td>12</td>
<td>30</td>
<td>9</td>
<td>0.40</td>
<td>Neves et al. (2005)</td>
<td></td>
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<tr>
<td>Houbara bustard <em>Chlamydotis undulata</em></td>
<td>Lanzarote, Spain</td>
<td>D</td>
<td>140</td>
<td>6</td>
<td>182</td>
<td>33</td>
<td>0.47</td>
<td>Lorenzo &amp; Ginovés (2007)</td>
<td></td>
<td></td>
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<tr>
<td>Houbara bustard</td>
<td>Fuerteventura, Spain</td>
<td>D</td>
<td>227</td>
<td>6</td>
<td>182</td>
<td>38</td>
<td>0.33</td>
<td>Lorenzo &amp; Ginovés (2007)</td>
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<td></td>
</tr>
<tr>
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<td>Castro Verde, Portugal</td>
<td>T</td>
<td>11</td>
<td>16</td>
<td>15</td>
<td>23</td>
<td>1.57</td>
<td>Marques et al. (2007)</td>
<td></td>
<td></td>
</tr>
<tr>
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<td>T</td>
<td>11</td>
<td>16</td>
<td>15</td>
<td>26</td>
<td>1.77</td>
<td>Marques et al. (2007)</td>
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<td></td>
</tr>
<tr>
<td>Great bustard</td>
<td>Ervidel, Portugal</td>
<td>T</td>
<td>5.8</td>
<td>12</td>
<td>15</td>
<td>6</td>
<td>1.03</td>
<td>Marques et al. (2007)</td>
<td></td>
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<tr>
<td>Great bustard</td>
<td>Castro Verde, Portugal</td>
<td>D</td>
<td>50</td>
<td>12</td>
<td>15</td>
<td>5</td>
<td>0.10</td>
<td>Marques et al. (2008)</td>
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<tr>
<td>Little bustard</td>
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<td>D</td>
<td>50</td>
<td>12</td>
<td>15</td>
<td>15</td>
<td>0.30</td>
<td>Marques et al. (2008)</td>
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<td>Ludwig’s bustard <em>Neotis ludwigii</em></td>
<td>Helios-Jun, South Africa</td>
<td>T</td>
<td>252</td>
<td>24</td>
<td>90</td>
<td>214</td>
<td>0.42</td>
<td>Shaw (2013)</td>
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<tr>
<td>Kori bustard <em>Ardeotis kori</em></td>
<td>Aries-Helios, South Africa</td>
<td>T</td>
<td>252</td>
<td>24</td>
<td>90</td>
<td>22</td>
<td>0.04</td>
<td>Shaw (2013)</td>
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</tr>
<tr>
<td>Karoo korhaan <em>Eupodotis vigorsii</em></td>
<td>Hydra-Kronos, South Africa</td>
<td>T</td>
<td>252</td>
<td>24</td>
<td>90</td>
<td>21</td>
<td>0.04</td>
<td>Shaw (2013)</td>
<td></td>
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</tr>
<tr>
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<td>D</td>
<td>29.7</td>
<td>mean 18 (range 8–31)(^2)</td>
<td>15</td>
<td>18</td>
<td>0.40</td>
<td>LPN (2012)</td>
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<tr>
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<td>Castro Verde, Portugal</td>
<td>D</td>
<td>29.7</td>
<td>mean 18 (range 8–31)(^2)</td>
<td>15</td>
<td>28</td>
<td>0.63</td>
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<td>T</td>
<td>126</td>
<td>1.3</td>
<td>11–13</td>
<td>2</td>
<td>0.15</td>
<td>Burnside et al. (2015)</td>
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<td>Bukhara, Uzbekistan</td>
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<td>114</td>
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<td>2</td>
<td>0.16</td>
<td>Burnside et al. (2015)</td>
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\(^1\)T, transmission; D, distribution.

\(^2\)Study consisted of a number of surveys, which varied in duration.
that bustards, including relatively small species, are vulnerable to mortality as a result of collisions with power lines. These studies varied in duration (2–24 months) and in population size and/or density, flight propensity and methods and frequency of searches for carcasses but yielded a mean of 0.69 detected bustard collision fatalities per km per year (range 0.04–3.21 km⁻¹·yr⁻¹).

Fifteen Bengal floricans with satellite transmitters were monitored until they had reached the flooding period and initiated non-breeding movements (Fig. 1b). In 2010 not all individuals undertook wet-season migration, whereas in 2011 13 moved to non-breeding areas and two died around the time of migration (Fig. 2). All 13 migrating individuals crossed the proposed route of the Tonle Sap power transmission line, typically twice in each non-breeding season, during outward and return movements (Fig. 2). However, some individuals’ breeding areas were overlapping or close to that proposed power line, indicating a potential to come into contact with the power line more frequently than just during seasonal movements (Fig. 1c).

Discussion

The annual adult survival rate of tagged Bengal floricans (89.9%) was comparable to that of other long-lived, slow-reproducing large bustards, such as the great bustard Otis tarda (90.9± SE 1.6%; Martin et al., 2007) and the Asian houbara Chlamydotis undulata (92.5%; Combreau et al., 2001). The limited satellite telemetry data available do not suggest age- or sex-related differences in movements or mortality. Of the six satellite-tagged Bengal floricans that died during the study three died in August or September, when the birds had moved a short distance from the breeding grounds but remained in the densely populated outer floodplain, where they are vulnerable to disturbance and hunting. The relatively high adult survival, along with low clutch size (1–2, typically one in Cambodia; Gray, 2008), suggests population dynamics will be sensitive to even a slight change in adult mortality rate, as indicated by demographic modelling for other bustard species (Combreau et al., 2001; Burnside et al., 2012; Dolman et al., 2015).

Migration routes between breeding and non-breeding areas crossed the proposed route of the Tonle Sap power line at least twice each year, with a few individuals that held breeding territories in close proximity to the transmission route crossing more frequently. The mean rate of bustard fatalities as a result of collision with power lines, from collated studies, was 0.69 per km per year. It is not possible to express this in terms of mortality risk per individual, as studies varied in population size, density, and probably in individual risk (in terms of timing and frequency of flights, and proximity to lines), which probably accounts for some of the variation in mortality rate detected. However, all studies were conducted where power lines crossed areas supporting concentrations of bustards (e.g. Alonso & Alonso, 1999; Marques et al., 2007; Jenkins et al., 2011; LPN, 2012; Burnside et al., 2015), broadly similar to the situation in Cambodia where subpopulations also vary in density and proximity to proposed power lines. Mortalities resulting from collisions with power lines have been shown to account for a significant proportion of non-natural deaths in a partially migratory population of great bustards, sufficient to influence population demography and behaviour (Palacín et al., 2016).

Demographic impacts of proposed power lines on the Bengal florican in Cambodia cannot yet be quantified, in part because there are insufficient data to quantify the demographic impacts of existing threats (e.g. hunting, nest predation, habitat loss and existing power lines). Nonetheless there is a risk that construction of the proposed Tonle Sap power transmission line will exacerbate ongoing declines and have a detrimental impact on the only significant population of the South-East Asian subspecies of Bengal florican.

Hotspots of high rates of collision with power lines are often reported in studies of avian mortalities (e.g. Shaw et al., 2010; Raab et al., 2012). Identification of areas of high collision risk facilitates targeting of mitigation measures to appropriate areas (Shaw, 2009). The proposed Tonle Sap power transmission line bisects one breeding site (Pouk) with at least five displaying males and passes within 1 km of Stoung–Chikraeng Bengal Florican Conservation Area, the only site with a stable population of Bengal floricans (Mahood & Channan, 2013). Of the c. 40 displaying males that use Stoung–Chikraeng, the density of birds is highest within a few kilometres of that proposed power transmission line (S.P. Mahood, pers. obs.). Male floricans make aerial displays (Collar et al., 2014) within an exploded lek (Davidson, 2004) and at the beginning of the breeding season aerial disputes for lek position can be seen daily (S.P. Mahood, pers. obs.). Birds are particularly vulnerable to collision with power lines during aerial displays (Henderson et al., 1996).

Although most non-breeding areas were located north of the proposed Tonle Sap power line, one satellite-tagged bird from Baray Bengal Florican Conservation Area spent a single non-breeding season in the vicinity of the proposed route for the Tonle Sap power line and it is likely that others would do the same in years where flooding is incomplete.

The proposed power transmission lines may also affect other vulnerable species. The breeding sites of the Bengal florican are used by a significant number of sarus cranes Antigone antigone, another species prone to collision (Sundar & Choudhury, 2005), and categorized as Vulnerable on the IUCN Red List. The cranes migrate into the floodplain annually from areas to the north of the proposed Tonle Sap power line. The waterbird colony at
Prek Toal, Battambang Province, is located c. 15 km from that proposed power line; the colony supports at least 40,000 pairs of large waterbirds, including five species of storks, half the global population of the Endangered greater adjutant \textit{Leptoptilos dubius} and the entire South-east Asian population of the Near Threatened spot-billed pelican \textit{Pelecanus philippensis} (Sun & Mahood, 2015). Elsewhere in the floodplain an additional two species of storks and a small population of the Critically Endangered white-shouldered ibis \textit{Pseudibis davisoni} also breed close to the proposed Tonle Sap power line. All of these large waterbirds disperse widely during the non-breeding season, rendering them vulnerable to collisions. The proposed power line from Kampong Thom to the international border with Laos PDR would pass through forest inhabited by three Critically Endangered vulture species and the Critically Endangered giant ibis \textit{Thaumatibis gigantea}. The route of the proposed power line from Kampong Cham to the Lower Sesan 2 hydropower dam is unknown but is likely to pass through areas where the white-shouldered ibis and other threatened species breed.

Mitigation measures to reduce the incidence of bird, and especially Bengal florican, collisions with the power lines were not included in the proposed designs but were recommended to the team developing the pre-EIA. Re-routing or burying power lines is considered to be the most effective mitigation measure for bird species that are particularly prone to collisions (Silva et al., 2014). Re-routing sections of the proposed Tonle Sap power line that are otherwise likely to become collision hotspots, such as that near Stoung-Chikreaeng Bengal Florican Conservation Area, is important for reducing the number of Bengal florican collisions with the line. Bird collisions with power transmission lines can usually be reduced through the use of bird flight deflectors or line markers, but with high-voltage transmission lines most signalling devices can only be used on the earth cables. The reduction in collisions by using marked cables can be as high as 78% (Barrientos et al., 2012); however, reductions are species-specific and there is a lower success rate for species with particularly constrained visual fields, such as bustards (Jenkins et al., 2010).

We recommend urgent research and consultation with stakeholders (Electricité du Cambodge, construction companies, financiers and communities) to identify appropriate areas where proposed transmission lines could be re-routed, and that appropriate line markers or bird-flight deflectors be installed along the entire network of power lines in Cambodia. As a result of multi-stakeholder consultations that used the analyses presented here, the construction company is considering installing bird-flight deflectors along the section of the power line closest to Stoung—Chikreaeng Bengal Florican Conservation Area. Given the likely impacts of the proposed power line on Cambodia’s globally important population of Bengal floricans and the risks to other threatened waterbirds, it is essential that these mitigation measures be adopted, and their effectiveness monitored.

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Author contributions

SPM conceived and wrote the paper, JPS collated bustard collision data, PMD edited the paper, and RJB analysed the satellite transmitter data and drew the figures.

References


Power cable threat to Bengal florican


Biographical sketches

Simon Mahood attempts to reconcile development interests with the conservation of threatened species. João Silva studies the ecology and conservation of steppe birds, and in particular the impacts of power lines on birds. Paul Dolman leads an interdisciplinary conservation ecology research team working on evidence-based biodiversity conservation in human-modified landscapes in Europe and Asia. Robert Burnside is a conservation biologist with a particular interest in ex situ management and translocations.