Seasonal landscape use and conservation of a critically endangered bustard: Bengal florican in Cambodia

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Contents

Abstract

The world's rarest bustard, the Critically Endangered Bengal florican *Houbaropsis bengalensis*, is found in two disjunct regions: the Indian subcontinent and South-East Asia. Two-thirds of the remaining population occupy the floodplain grasslands of the Tonle Sap lake, Cambodia. Producing an up-to-date landcover map of this area enabled recent habitat changes to be assessed. Nearly a fifth of the grassland in the key remaining area was lost in just four years (2005–2009) to intensive commercial rice cultivation. To date, research and conservation efforts have focused on the distribution and habitat of male floricans during the core breeding period (mid-February–early June). However, at the onset of the wet season, the floricans' grassland habitat floods, and their movements, distribution, habitats and threats are poorly understood. Using satellite-telemetry, movements of both sexes (from five breeding sites) were tracked throughout the year. When breeding, home ranges were an order of magnitude larger than previously determined from radio-tracking. Females had larger home range core areas than males, and pre- and post-breeding movements were wider than during the core breeding period. Current protected areas may therefore be insufficient. Grassland was the only habitat type selected and smaller home ranges contained a higher proportion of grassland cover. Wet season migration is facultative: some birds remain if the breeding grasslands are sufficiently dry. Floricans were strongly site faithful in both breeding and non-breeding ranges. Migratory floricans were tracked to non-breeding areas, up to 42 km from breeding sites. Birds from three northern and two southern breeding sites did not overlap in non-breeding areas. Floricans favour open savanna habitat and avoid agriculture and closed-canopy forest. Different conservation approaches are required for the northern and southern areas. In the north suitable habitat remains but is threatened by plantations. The location of protected areas needs reconsideration as they were little used by tagged birds and contained much unsuitable habitat. In the south, land is dominated by agriculture: habitat restoration and protection are required.

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Chapter 1: General introduction

Knowledge constraints on effective conservation

Effective conservation of a threatened species requires a thorough understanding of its ecology. However, for many rare species, particularly in the tropics, this knowledge has never been generated and is difficult to obtain owing to behavioural, environmental, logistical and/or socio-political factors. Increasingly, however, technological advances are helping to overcome these constraining factors, providing a means of investigating aspects of species' biology that were not previously accessible to scientific study. A major example of this are the developments made in remote sensing, with satellites providing a means to track the movements of individuals fitted with transmitters, as well as to produce high resolution images of large areas of land. Both of these applications of remote sensing are rapidly becoming indispensable tools in conservation biology.

Satellite-tracking systems have hugely improved our understanding of animal movement patterns. As technology has advanced, transmitter size has decreased, opening up the application of satellite-tracking to a growing number of species. This has facilitated substantial progress in the understanding of migratory patterns, routes and destinations of little known and difficulty-to-study species, and proved an important tool in gaining information necessary for the effective conservation of threatened species (Hebblewhite and Haydon, 2010).

Similarly, as the resolution of satellite imagery has improved, its usefulness for conservation biology has increased (Turner et al., 2003). Detailed and up-to-date landcover maps often do not exist where they are most needed, in areas with the richest biodiversity facing the greatest threats. It is highly unlikely that the necessary information required to meet these threats can be obtained by field-based methods alone (Heywood, 1995), although clearly it is important to support remotely sensed data with field-based measures (Kerr and Ostrovsky, 2003). Mapping habitat across large landscapes on foot is hugely time-consuming, expensive and difficult to keep updated, and is particularly problematic (and important) in landscapes undergoing rapid change (Bock, 2003). The use of satellite imagery to map habitats is far more efficient, can be regularly updated and is increasingly affordable. Progressively finer resolution satellite images are available; and although higher-resolution images are still prohibitively expensive, Landsat 7 ETM+ images are now free, and with a resolution of 30 x 30 m they have many useful applications. These include: mapping habitat covers and landuse change, determining habitat correlates of species distributions, and identifying potential areas of suitable/important habitat to guide subsequent field-based surveys (improving efficiency).

Threatened migratory species arguably present the greatest challenge, both to obtaining adequate knowledge of the threats they face and their year-round ecological needs, and to developing conservation solutions that will overcome the threats and meet these needs (Martin et al., 2007). For migratory species a habitat- or site-based approach is rendered increasingly complex by the number of sites and perhaps habitats that they occupy throughout the year, and their survival will instead depend on the successful tackling of all the spatial and temporal problems that face them through the annual cycle (Webster et al., 2002).

With 10,158 animal species listed as threatened and 7,976 as Data Deficient (IUCN Red List of Threatened Species, 2011), clearly it is not practical to take a single-species approach for all of them (Collar, 1994; Myers et al., 2000). However, even when conservation measures are targeted at single threatened species, a number of other species are very likely also to benefit (Lambeck, 1997); and measures targeted at appropriate umbrella species can benefit important assemblages. In Cambodia, efforts to protect the seasonally inundated grassland habitat of a Critically Endangered bustard, the Bengal florican *Houbaropsis bengalensis*, will also benefit 10 other globally threatened bird species (see Chapter 2) and a rich diversity of fish and herpetofauna that inhabit the floodplain (Campbell et al., 2006).

Conservation in anthropogenic landscapes

Pristine areas of natural habitat are most highly valued and have received much attention from researchers and conservationists (Dove, 2004). However, recognition of the importance of anthropogenic landscapes for biodiversity is growing (Oldfield and Alcorn, 1987; Plieninger and Wilbrand, 2001; McNeely and Schroth, 2006; Plieninger et al., 2006; Bhagwat et al., 2008). Tropical grasslands are one of the most highly threatened ecosystems (Sala et al., 2000; Millenium Ecosystem Assessment, 2005; Hails et al., 2006; Bond and Parr, 2010). They support unique wildlife assemblages and are of considerable importance for biodiversity, yet their association with people has often led them to be relatively undervalued (Collar, 1996a; Dove, 2004). Whilst human activities in grasslands can pose serious threats (e.g. Villamil et al., 2001), they can also be a fundamental tool in preserving and even creating habitat (Pons et al., 2003): it is increasingly recognised that many grassland ecosystems and grass-savannas in North America, Australia, Africa and Asia are entirely anthropogenic in origin, with fire and grazing key to controlling encroaching woody vegetation. Other apparently natural grassland areas have historically been maintained by wild herbivores, whose grazing prevents succession to

scrub and forest. However, in many areas these species no longer persist, but their role has been continued by domestic cattle. Skills and understanding of grassland management techniques have grown, but have mostly focused on temperate rather than tropical grasslands.

Traditional low-intensity agro-ecosystems supporting biodiversity are threatened by both intensification and abandonment (Plieninger et al., 2006). However, the debate over the alternative conservation approaches of landsharing (low-intensity agriculture that supports wildlife) and landsparing (high-intensity agriculture that requires less land and therefore leaves non-agricultural areas available for wildlife) continues (Green et al., 2005; Hodgson et al., 2010; Phalan et al., 2011). As the pressure to increase food production grows, finding a balance between agriculture and biodiversity conservation will become even more important and challenging (Green et al., 2005).

Bustards (Otididae)

Bustards are essentially grassland species, but some will utilise areas of partial scrub and tree cover whilst others make use of semi-desert habitat (Collar, 1996b). They also show varying degrees of tolerance to low-intensity agriculture (Collar, 1996b; Salamolard and Moreau, 1999; Aghainajafi-Zadeh et al., 2010). Bustards are widely distributed, occurring in Europe, Asia, Africa and Australia. They are generally K-selected, with long adult life expectancy and low fecundity. These long-legged, long-necked birds tend to walk more than fly, and roost and nest (the young are precocial) on the ground. They are omnivorous, but dependent on insects to feed chicks.

Bustard plumage is generally rather cryptic, although males are often brighter and develop ornamental features used in display in the breeding season (Collar, 1996b). Females are expert in concealment, especially during the breeding season, when their camouflaged plumage and secretive behaviour help to evade the attention of predators. Many bustards exhibit sexual size dimorphism, which however is in the reverse direction (females larger than males) in the two florican species (*Houbaropsis bengalensis* and *Sypheotides indica*). Bustard mating systems are unusual, with many having (or presumed to have) 'exploded leks': males hold individual territories (where they display and feed), but these are clustered together within a landscape (Collar, 1996b). They also tend to be strongly site-faithful (Alonso et al., 2000, 2009; Judas et al., 2006; Palacín et al., 2009). Varying degrees of migratory behaviour are recorded in bustards, both within and between species, but movement patterns are still being clarified by

ongoing research (Combreau et al., 1999, 2011; Alonso et al., 2000, 2009; Morales et al., 2000; Judas et al., 2006; Streich et al., 2006; Palacín et al., 2009, 2011; Villers et al., 2010).

The bustard family has a disproportionately high number of threatened species (Collar, 2009), with almost half of the 25 species listed as globally Threatened or Near Threatened (Table 1). Habitat loss, landuse intensification and hunting have been the majors drivers in their decline.

Studying bustards presents many challenges: they are wary of people and many have a well-camouflaged plumage (limiting field observations), they are difficult to capture (for marking or deploying tracking devices) and many inhabit remote and inhospitable landscapes that are difficult to access (Collar, 1996b). In recent years, advances have been made in catching and tracking bustards which have helped to shed light on many aspects of their ecology that could not previously be studied. To date, houbara *Chlamydotis undulata*, great bustard *Otis tarda*, little bustard *Tetrax tetrax*, Australian bustard *Ardeotis australis*, kori bustard *A. kori* and Bengal florican have been tracked with radio and/or satellite telemetry (Osborne et al., 1997; Alonso et al., 2000, 2009; Morales et al., 2000; Hingrat et al., 2004, 2006; Judas et al., 2006; Martín et al., 2008, 2007; Palacín et al., 2009; Gray et al., 2009; Villers et al., 2010; Ziembicki, 2010; Magaña et al., 2010; Combreau et al. 2011; Senyatso, 2011). This has improved understanding of between- and within-season movements and home ranges, of differences in movement patterns between regions, populations and sexes, and of mating systems, nesting ecology, site fidelity and habitat preferences.

Table 1. Globally Threatened and Near Threatened bustard species (IUCN Red List of Threatened Species, 2011).

Scientific name	Common name	IUCN red list status
Ardeotis australis	Australian Bustard	Near Threatened
Ardeotis nigriceps	Great Indian Bustard	Critically Endangered
Chlamydotis undulata	Houbara Bustard	Vulnerable
Eupodotis caerulescens	Blue Bustard	Near Threatened
Eupodotis humilis	Little Brown Bustard	Near Threatened
Houbaropsis bengalensis	Bengal Florican	Critically Endangered
Neotis denhami	Denham's Bustard	Near Threatened
Neotis ludwigii	Ludwig's Bustard	Endangered
Neotis nuba	Nubian Bustard	Near Threatened
Otis tarda	Great Bustard	Vulnerable
Sypheotides indicus	Lesser Florican	Endangered
Tetrax tetrax	Little Bustard	Near Threatened

The Bengal florican *Houbaropsis bengalensis*

The Bengal florican is the rarest of the bustard species and the only member of the genus *Houbaropsis* (Table 1). It has a disjunct distribution, with a population in the Indian subcontinent and another in South-East Asia. The Bengal florican is split into two subspecies: *H. b. bengalensis* found in India and Nepal, and *H. b. blandini* found in Cambodia and Vietnam. *H. b. blandini* is morphologically distinct (described as having a shorter bill with a heavier base, richer plumage coloration and, in males, shorter ornamental feathers on the head and neck: (Delacour, 1929), and it seems very likely to have been separated from the nominotypical form found in India and Nepal for a very long time. In India, the Bengal florican is distributed from the Kumaon terai of Uttar Pradesh to Bihar and West Bengal and the foothills and plains of Arunachal Pradesh, Assam and Meghalaya, and in Nepal it is found in the terai (BirdLife International, 2001). Floricans also historically occurred in Bangladesh. In South-East Asia, the Cambodian population was only rediscovered by scientists in 1999 (Goes and Sam Veasna, 1999) and is mostly found in the floodplain of the Tonle Sap lake, with 62% in Kompong Thom Province (Gray, 2008), whilst the population previously found in southern Vietnam may now be extinct. Population estimates are: India, no recent population estimate but likely to be fewer than 250 birds (based on estimates between 1990 and 2000), Nepal 28–36 adults in 2007 (Poudyal et al., 2008; Donald et al., 2010), Cambodia 666–1004 in 2005 (Gray et al., 2009) and no recent confirmed records from Vietnam. Since 2005 there has been extensive conversion of florican breeding grasslands in Cambodia's Tonle Sap floodplain and therefore

the population is likely to have declined (Gray et al., 2009, also see Chapter 2). It would seem highly likely that the total global population in now fewer than 1000 individuals, and could well be considerably lower.

In Cambodia, floricans breed in the seasonally inundated grasslands surrounding the Tonle Sap lake (Gray et al., 2009, Figure 1). The Tonle Sap Lake covers approximately 2,500 km^2 in the dry season, expanding up to 15,000 km^2 in the wet season, when rising levels in the Mekong River force water back up the tributary Tonle Sap River (seasonally reversing the direction of flow) into the lake. (Campbell et al. 2006). Large expanses are burned by local communities, promoting re-growth for grazing cattle. It is within these burnt areas that males often defend territories, which are clustered together to form an exploded lek (Gray et al., 2009). Males perform flight displays from February to early June (Davidson, 2004), most intensely at dawn and dusk (C. Packman pers. obs.). The larger females are very secretive, tending to prefer taller vegetation (Gray et al., 2009). Females visit male territories to mate, after which the males have no further involvement. Eggs are laid on a bare patch of ground, usually beside taller patches of vegetation. In Cambodia a single egg is most common, although two are sometimes laid (Gray, 2008), whereas in India, two-egg nests are more frequent (Bombay Natural History Society, 1990). Incubation is believed to last 25–28 days (Collar, 1996b) before the precocial chicks hatch. The period of post-natal dependence is not known.
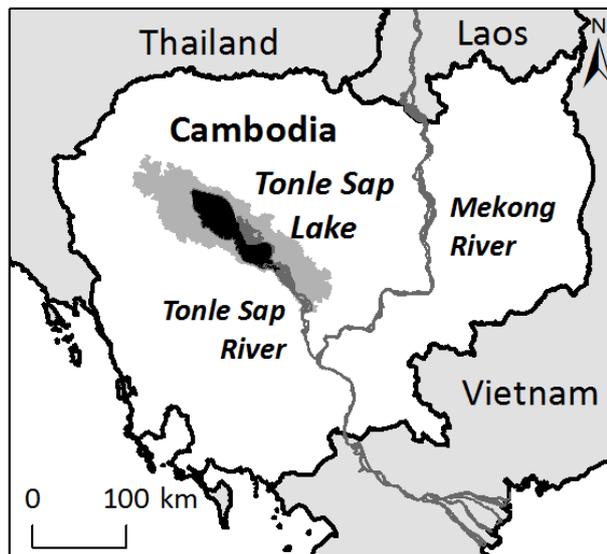
Figure 1. Location of the Tonle Sap Lake, Cambodia, showing dry season (black) and wet season (dark grey) extent.

Formerly, hunting pressure in Cambodia is believed to have been high (and historically in India too, where it was called '*Otis deliciosa*', Collar, 1996b), with an estimated 300–600 birds sold annually in a single market located 15 km from the nearest grassland (Sam Veasna, 1999). Whilst some hunting still occurs (see Chapter 3), it is now much less evident. The major threat now comes from rapid habitat conversion in the floodplain breeding grounds (Gray et al., 2009 and Chapter 2). In response, the Forestry Administration of Cambodia, Wildlife Conservation Society and BirdLife International in Indochina developed 'Integrated Farming and Biodiversity Areas' (now renamed Bengal Florican Conservation Areas: BFCAs), which were designated in 2006 and 2007 to protect grassland areas (van Zalinge et al., 2009). Construction of new dams for irrigated rice is not permitted within the BFCAs, where co-management frameworks with local communities are being developed, encouraging beneficial traditional landuses to continue.

Bengal florican in Cambodia: research context

Research conducted by Davidson (2004) revealed the importance of the Cambodian population and examined male breeding ecology and habitat requirements as well as vegetation and landuse aspects at three key sites in Kompong Thom Province. This was built on by Gray (2008), who improved understanding of the distribution and population size of floricans in Cambodia, drew attention to the threats of both agricultural abandonment and intensification, emphasised the benefits of low-intensity agricultural practices, and improved our understanding of both male and female breeding habitat preferences using radio telemetry. This thesis builds in turn on Davidson's and Gray's work and aims to address some of the remaining unanswered questions of the species's ecology that will be crucial for informing conservation measures. A key gap in the knowledge base is the lack of information and understanding of florican movements, distribution and habitat requirements during the non-breeding (wet) season. This was highlighted by both Davidson (2004) and Gray (2008) as an important area of this species's ecology that requires research in order to inform conservation measures that will benefit this species throughout the annual cycle.

Thesis aims

This thesis first assesses rates of grassland loss in the Tonle Sap floodplain, bringing previous estimates up to date. At the last assessment, rapid conversion of grassland to intensive commercial agriculture was reported between 2005 and 2007 but was not well quantified

owing to limitations in field-based mapping of habitats (Gray, 2008). Although this threat has been perceived since then to be growing, there has been no subsequent quantitative assessment. Given the great important of these grasslands for the Bengal florican population, as well as a number of other threatened species, an updated estimate of remaining grassland area was urgently needed and this is addressed in Chapter 2. When the breeding grasslands flood during the wet season, movements and distribution of floricans are poorly understood. Chapter 3 reveals the timing and patterns of wet season migration and identifies localities used by floricans during this part of the year. Using the information gained from tracking floricans to wet season areas, Chapter 4 examines habitat preferences in the non-breeding season, habitat change and landuse implications for conservation. Previous florican research by Davidson and Gray focused on male breeding ecology. Whilst females were also radio-tracked by Gray, the results suggested females may leave the exploded lek areas occupied by males, so understanding their breeding distribution and spatial requirements required further research. Chapter 5 examines breeding season spatial and temporal patterns of home range occupation and habitat use using satellite telemetry, to gain a better understanding of the movements of both sexes. In addition, pre- and post-breeding movements are assessed, neither having previously been studied. Chapter 6 concludes with a discussion of key findings, the use of remote sensing technology and conservation implications and recommendations from this study.

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Chapter 2:

Accelerating loss of Southeast Asia's last major flooded grassland biome

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Abstract

Tropical flooded grasslands are among the world's most highly threatened biomes. In Southeast Asia they are of high biodiversity value but have almost entirely disappeared. The largest remaining area is found in the extensive floodplain (c. 11,000 km^2) of the region's biggest lake, the Tonle Sap, Cambodia. The Tonle Sap grasslands are of considerable importance to biodiversity, supporting 11 globally threatened bird species, yet rates of loss have not previously been documented. Nearly half (46%) of the grassland was lost in the ten years to 2005, driven by scrub encroachment following agricultural abandonment. Subsequently, extraordinarily rapid expansion of industrial-scale dry season rice production has destroyed 19% of grassland remaining in the key area, in just four years. This high-speed conversion has intensified pressure on already threatened species and on the marginalised rural communities dependent on the grassland ecosystem. The loss of this entire biome from Southeast Asia is imminent without immediate intervention.

Keywords: Flooded grassland, tropical grassland, scrub encroachment, agricultural abandonment, agricultural intensification, irrigated rice, Tonle Sap, Bengal florican

Introduction

Tropical and flooded grasslands are among the most threatened biomes globally (Sala 2000; Bond & Parr 2010; Millenium Ecosystem Assessment 2005). However, rates of loss are poorly documented (Jenkins et al. 2003), in contrast to forests (Hansen et al. 2010; FAO 2005). Many tropical grasslands are anthropogenic or human-modified ecosystems, influenced by livestock grazing and burning (Lambin et al. 2001; Bredenkamp et al. 2002). Changes in the type and intensity of such activities can have considerable impacts, making grasslands susceptible to both intensification and abandonment of land-use. The susceptibility of grasslands to scrub encroachment is a worldwide phenomenon (Sankaran et al. 2004; Eldridge et al. 2001). Scrub invasion can occur when grazing and fire intensity decrease or conversely through over-grazing, and associated changes in fuel loads that alter fire frequency and intensity (Bredenkamp et al. 2002; Rogues et al. 2001; Riginos & Young 2007). Tropical grasslands are also highly vulnerable to conversion to agriculture (e.g. Maria et al. 2002), driven by escalating demand for production.

Tropical flooded grasslands are highly productive and dynamic environments, important for both biodiversity and ecosystem services (Wikramanayake et al. 2001). The seasonally inundated grasslands of Southeast Asia support distinctive assemblages and globally threatened species, but are particularly highly threatened (BirdLife International 2007). With the loss of almost all such habitat from Thailand (Round 2002) and Vietnam (Tran Triet et al. 2000; Buckton & Safford 2004), the floodplain of Cambodia's Tonle Sap Great Lake (Fig. 1) holds the largest remaining seasonally inundated grassland in Southeast Asia (BirdLife International 2003). The Tonle Sap Lake expands to cover up to 15,000 km^2 in the wet season, when rising levels in the Mekong River force water back up the tributary Tonle Sap River into the lake. In the dry season, the lake's area recedes to approximately 2,500 km^2, as falling levels in the Mekong allow outflow to resume down the Tonle Sap River (Campbell et al. 2006).

The grasslands of the Tonle Sap floodplain are of major importance for biodiversity, being used by eleven globally threatened bird species (Table 1) including two-thirds of the world population of the Critically Endangered Bengal florican (*Houbaropsis bengalensis*) (Gray et al. 2009). When inundated, the floodplain is also vital to fisheries (forming a spawning ground), to a high diversity of water snakes (including a threatened endemic) and to waterbirds (Campbell et al. 2006;

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Mekong River Commission 2010). The immediate surroundings of the lake are inhabited by 1.1 million people (Varis et al. 2002), with the grasslands providing pasture as well as supporting traditional low-intensity rice cultivation and fisheries in seasonal pools (Diepart 2007; Keskinen et al. 2007).

However, private businesses are now converting the grasslands to intensive commercial rice cultivation. This land-use change has been so rapid that local communities and conservationists have struggled to oppose, mitigate or even document it. Here we provide the first quantitative assessment of remaining grassland extent and rates of conversion, highlighting the scale of loss and the urgency of intervention needed to secure this rapidly vanishing biome.

Methods

We assessed habitat conversion across the Tonle Sap floodplain by relating landcover manually delineated from January/February 2005 aerial photography (1:25,000; Pasco-Finnmap 2005) to landcover for 1995/6 derived from combined satellite imagery (LANDSAT and SPOT), aerial photography (1:25,000 and 1:40,000) and topographic maps (1:50,000) (JICA 2000). By 2005, much of the remaining grassland was concentrated in the southeastern section of the floodplain. To quantify post-2005 grassland conversion in this latter region, we updated landcover data by supervised classification of February 2009 LANDSAT imagery (30x30 m pixels) using ground-truth data (740 training points and 189 validation points) from across this area (2,407 km^2, see Supporting Information for method details).

For all three mapping periods, landcover was consistently classified as: grassland, scrub, wetland, wet season rice, dry season rice or other (mainly small areas of non-rice crops and flooded forest patches irrelevant to this assessment). Traditional, locally practiced 'wet season rice' cultivation provides fallows and stubbles used by grassland biota during the dry season. It comprises rain-fed rice in bunded fields in the peripheral floodplain and lower-intensity deep-water rice in areas that flood to greater depths. In contrast, commercial, privately financed 'dry season rice' is intensively cultivated after floodwaters subside, through the construction of dams, channels and reservoirs to provide irrigation water.

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Because they have contrasting potential for land-use conversion, two types of grassland were differentiated: 'wet grassland', typical of inner floodplain areas and experiencing deeper flooding of longer duration, and 'dry grassland', typical of outer floodplain areas subject to a shallower flood of shorter duration. Differing flood conditions are reflected in floodplain soil types. Therefore dry and wet grassland were identified by overlaying a soil classification map (Sokha 2003) on the grassland areas depicted by landuse maps. Grassland on gleysols (largely occurring in the inner floodplain) was classified as wet grassland, that on plinthosols, acrisols, cambisols, luvisols and fluvisols (characteristic of the outer floodplain) were classified as dry grassland. These represent different communities, with wet grassland often dominated by the grasses *Oryza rufipogon* and *Leersia hexandra* and dry grasslands consisting of *Rhynchospora* sedges, *Arundinella setosa*, *Eragrostis atrovirens*, *E. brownii* and *Imperata cylindrica* (Davidson 2004)*.

Results

In 1995/6, grassland was extensive, covering 3,349 km^2 (30%) of the floodplain (Fig. 2A). By 2005 this had reduced to 1,817 km^2, a net loss of 1,532 km^2 (46%) in 10 years. Heaviest losses occurred in the north and west and in inner areas (Fig. 2B). Wet grassland experienced the greatest loss (64%) which, combined with 23% loss of dry grassland, meant that grassland had almost disappeared from much of the floodplain by 2005. The only exception was in the southeastern section where 81% of the 1995 grassland area (85% of it dry grassland) remained in 2005 (Fig. 2C and D). Across the floodplain, scrub cover increased by 23% from 1995/6 to 2005 and was the major source of grassland loss. Gains from former scrub areas were inconsequential (Fig. 3A). Some grassland in the outer floodplain was lost to wet season rice, offset by wet season rice that reverted to grassland.

In the southeast floodplain, grassland area was subsequently reduced by 19% in just four years (from 923 km^2 in 2005 to 751 km^2 by 2009). Of this loss, 95% was attributable to intensive dry season rice cultivation (84%) and associated areas of wetland within reservoirs (11%). In 2005, areas of dry season rice emerging in former grassland areas were small (Fig. 2D) but over the next four years increased by 666%, from 50 km^2 in 2005 to 383 km^2 in 2009 (Fig. 2E). Gains and losses

between grassland and wet season rice or scrub were approximately equal over this period (Fig. 3C).

Discussion

Historically, traditional agricultural activity is likely to have checked scrub encroachment in the remote inner floodplain areas, where pastoralists grazed cattle on productive wet grassland during the dry season and local communities cultivated deep water rice; both landuses are associated with scrub clearance and dry season burning. However, with economic and political changes, local communities have become increasingly sedentarised in peripheral villages, grazing their cattle daily on outer floodplain grasslands and abandoning the inner floodplain, leaving it highly susceptible to scrub encroachment.

The already rapid and extensive loss of flooded grassland through abandonment and succession has now been compounded by the advent of industrial-scale intensive dry season rice cultivation in the remaining areas of grassland. The private, often illegal enterprise of growing dry season rice has usurped customary land-use rights of grazing and traditional rice cultivation, at the expense of the poorest local communities (Diepart 2007; Keskinen et al. 2007; World Bank 2006; Evans & Prak 2008; LICADHO 2009). The Tonle Sap is the second poorest agro-ecological zone in Cambodia, with 33% of the human population below the national poverty line in 2004 (World Bank 2006). With Cambodia's food aid needs for 2011 being valued at more than US$31 million it has been observed that "rising inequality and landlessness and deterioration of common property resources have eroded the coping capacity of food-insecure people" (World Food Programme 2011). Much of this dry season rice production is for other nations' food security, with further large areas of land under lease negotiation with Kuwait, Qatar (Economist 2007) and China (Marks 2011).

The massive reduction in this grassland's extent has severe implications for biodiversity, most notably for the world's largest remaining population of Bengal florican. Currently only 173 km^2 (23%) are under some form of protection. Parts of these protected areas have already been lost to dry season rice developments and are highly vulnerable to further conversion. Recent condemnation of illegal dry season rice dam constructions by the Cambodian government (fearing

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impacts on fish stocks), along with the demolition of some dams in 2010 (Phann & Vrieze 2010), is a positive sign but insufficient in itself. Grassland capable of supporting Bengal florican and other threatened bird species can regenerate within one/two years following abandonment of wet season, deep-water rice fields (Gray 2008), but recovery from intensive mechanised cultivation of dry season rice is likely to be slower. Only a strong political commitment to protection and restoration can now prevent the impending loss of the flooded grassland biome from Southeast Asia.

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Table 1. Globally threatened bird species occurring in the Tonle Sap grasslands.

Scientific name	Common name	IUCN Red List status	Grassland status
Houbaropsis bengalensis	Bengal florican	Critically endangered	Breeding
Pseudibis davisoni	White-shouldered ibis	Critically endangered	Breeding
Leptoptilos dubius	Greater adjutant	Endangered	Non-breeding
Grus antigone	Sarus crane	Vulnerable	Non-breeding
Aquila clanga	Greater spotted eagle	Vulnerable	Non-breeding
Aquila heliaca	Imperial eagle	Vulnerable	Non-breeding
Pelecanus philippensis	Spot-billed pelican	Vulnerable	Non-breeding
Mycteria cinerea	Milky stork	Vulnerable	Non-breeding
Leptoptilos javanicus	Lesser adjutant	Vulnerable	Non-breeding
Acrocephalus tangorum	Manchurian reed warbler	Vulnerable	Non-breeding
Emberiza aureola	Yellow-breasted bunting	Vulnerable	Non-breeding
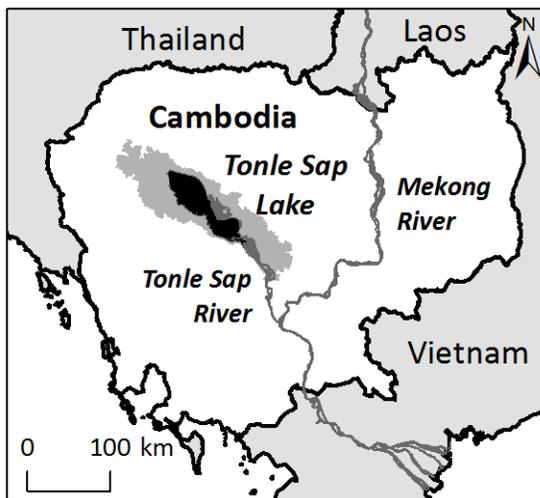
Fig. 1. Location of the Tonle Sap Lake, Cambodia, showing dry season (black) and wet season (dark grey) extent.
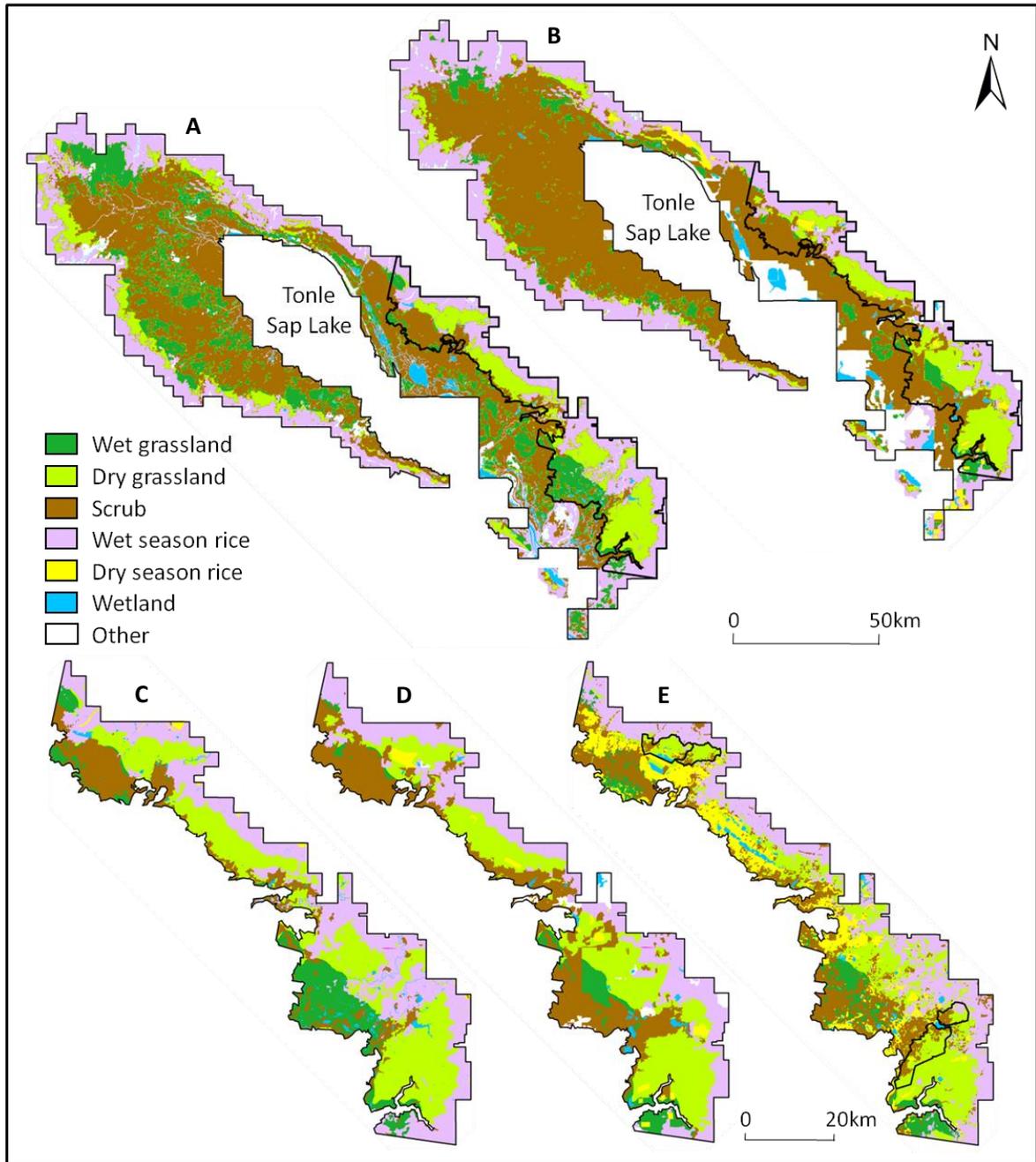
Fig. 2. Landcover for the Tonle Sap floodplain (11,187 km^2) in (A) 1995/6 (from JICA 2000) and (B) 2005, and for the southeastern section (2,407 km^2, outlined in maps A and B) in (C) 1995/6, (D) 2005 and (E) 2009 (with protected areas delineated in black).
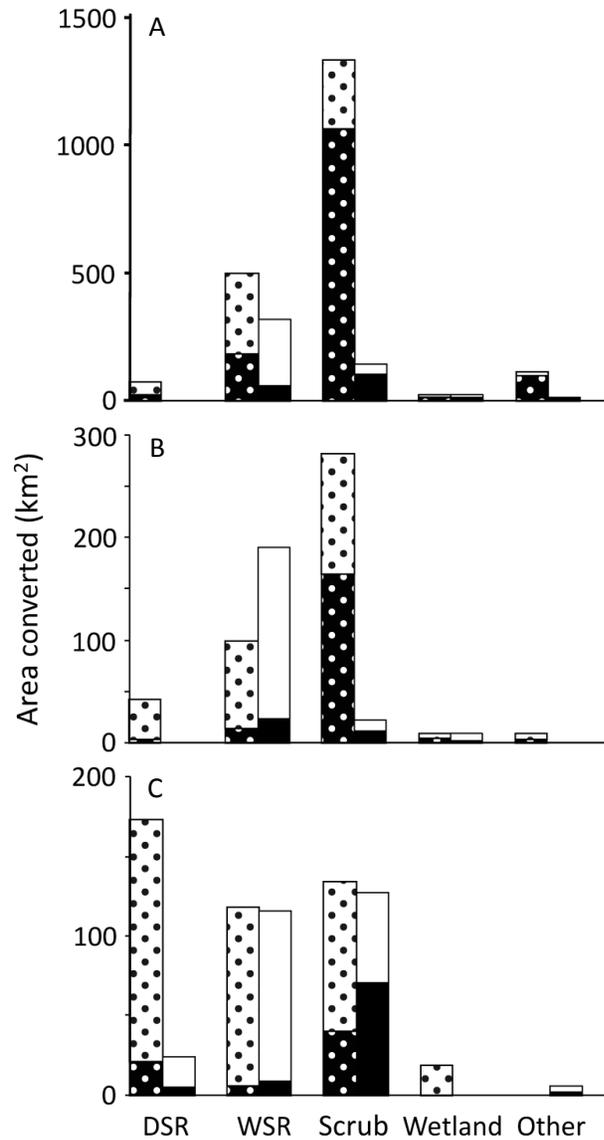
Fig. 3. Land area transitions between 1995/6 and 2005 of wet (black) and dry (white) grassland either to (stippled) or from (plain) dry season rice (DSR), wet season rice (WSR), scrub, wetland or other landuse for (A) the whole Tonle Sap floodplain (11,187 km^2, with 495 km^2 of wet and 820 km^2 of dry grassland unchanged during this period), (B) the southeastern section of the Tonle Sap floodplain (2,407 km^2 with 99 km^2 of wet and 601 km^2 of dry grassland unchanged) and (C) for the four years between 2005 and 2009 for the southeastern floodplain (with 69 km^2 of wet and 409 km^2 of dry grassland unchanged).

Supporting Information

Detailed methods

Analysis of remote sensing data

The Cambodia Reconnaissance Survey Digital Data project (JICA 2000) consisted of two phases, with Phase 1 using data from 1995/6 and covering the Tonle Sap region of Cambodia. The accuracy of the landcover map was reported to be around 80% (JICA 2003) and is widely accepted as the most reliable landcover map for this period. For comparison with the 2005 and 2009 maps, the 1995/6 landcover types (JICA 2000) occurring within the Tonle Sap floodplain were combined into broad habitat categories as shown in Table S1. Selection of these habitat categories was based on prior knowledge of the area, the likely major habitat transitions in and around grassland areas, and habitat types that could be consistently classified from more recent LANDSAT imagery.

Habitat cover for 2005 was determined by manual interpretation and digitization of 1:25,000 aerial photographs (from Pasco-Finnmap 2005). The habitat types identified correspond with the habitat categories assigned to the 1995/6 landuse map listed in Table S1. Accuracy was validated using 100 randomly selected ground-truth plots of 10 km^2, 96% of which were correctly classified.

To update landcover data for 2009 for the southeastern section of the Tonle Sap floodplain, a LANDSAT 7 ETM+ scene from February 2009 was obtained. A February image was used as it was cloud-free and in the dry season, so the floodwaters had receded, exposing underlying habitat types. As all post-2003 LANDSAT images have some data missing (as a result of the failure of the scan-line corrector on the satellite in May 2003), gaps in the image were partially filled using a local linear histogram matching technique with an image from the previous month (following Scaramuzza et al. 2004). This approach was validated by comparing pixel values for the same location obtained from each of the two images (January and February 2009); generating 1000 random points in ArcMap 9.2 (ESRI 2006), and excluding any point for which data were missing in either month. Mean absolute errors between the pixel values for the two images were assessed for each band and found to be minimal in comparison to the spatial variation within the February 2009 image (Table S2). Complete filling of the data gaps was achieved by subsequently applying

neighbourhood mean calculations, with a 3x3 pixel window, iterated three times. The image for each LANDSAT 7 spectral band was examined and bands three, four, five, and seven were selected as they showed the greatest image contrast, feature definition and encompassed a range of spectral properties (Table S3.)

A total of 929 ground-truthing points were selected by stratified (according to habitat and unsupervised classification categories) random sampling. Of these, 740 were used as training points to produce a supervised habitat classification (maximum likelihood) using Spatial Analyst Tools in ArcMap 9.2. To reduce the number of isolated, incorrectly classified pixels, smoothing was applied with a majority filter. This used a 3x3 pixel window around the central pixel (the eight neighbouring cells). A replacement threshold of half meant that of the eight neighbouring cells four must be of the same value and connected to replace the central pixel. This process was repeated until the maximum classification accuracy was achieved. The accuracy of the classification was assessed using the remaining 189 ground-truthed points, randomly selected from each habitat. The overall accuracy of the classification (proportion of validation points correctly classified) was 77%. A KHAT statistic (which indicates the extent to which the percentage of correct values are due to 'true' rather than 'chance' agreement; Lillesand et al. 2008) of 0.67 was obtained. Producer's Accuracies (proportion of correctly classified validation points for each habitat category: Lillesand et al. 2008) are listed in Table S4. Manual corrections were subsequently applied to areas (totalling 20 km^2) of known habitat type that had been incorrectly classified, thus further improving the map. Changes in grassland area and habitat transitions for 1995/6, 2005 and 2009 were assessed in ArcMap 9.2 (Environmental Systems Research Inc 2006).

Supporting Tables

Table S1. Habitat categories assigned to 1995/6 landcover types occurring within the Tonle Sap floodplain.

1995/6 landcover category	Habitat category assigned
Open water	Wetland
Lake or pond	
Dense forest / jungle	
Clear forest	
Shrubland	Scrub/Forest
Flooded shrub	
Flooded forest	
Flooded grassland	
Marsh or swamp	Grassland
Grassland	
Rice field	Wet season rice
Receding and floating rice fields	
Field crops	
Village garden crops	
Swidden agriculture	Other
Plantation	
Urban	

Table S2. Mean absolute error in pixel values between February 2009 (main) and January 2009 (fill) LANDSAT 7 ETM+ tiles from 1000 randomly generated points. Mean pixel values and their standard deviations for February 2009 points are also given as a reference. Pixels have a minimum value of zero and a maximum value of 255.

Band number	Mean absolute error in pixel value and standard deviation	Mean pixel value and standard deviation for February 2009 tile
3	3.1 ± 4.0	61.9 ± 17.1
4	3.0 ± 3.5	59.7 ± 11.9
5	6.8 ± 7.8	84.8 ± 32.7
7	5.3 ± 6.4	51.8 ± 25.8

Table S3. LANDSAT 7 ETM+ spectral bands and their uses (Lillesand et al. 2008).

Band number	Spectral band	Use
3	Visible Red	Indicates chlorophyll absorption
4	Near Infrared	Emphasises biomass content and water bodies
5	Mid Infrared	Highlights moisture content of soil and vegetation
7	Mid Infrared	Discriminates mineral and rock types, also sensitive to vegetation moisture content

Table S4. Producer's Accuracies by habitat category for the supervised habitat classification using 189 independent validation points.

Habitat category	Producer's Accuracy (%)
Grassland	76
Dry season rice	64
Wet season rice	86
Scrub	60
Wetland	95

Chapter 3:

Wet season migration and distribution of Bengal floricans in
Cambodia: patterns, timing and implications for conservation

Abstract

The largest remaining population of a Critically Endangered bustard, the Bengal florican, is found in the floodplain of the Tonle Sap lake, Cambodia. The location of floricans during the wet season, when these sites are flooded, was previously poorly understood. With the use of satellite telemetry we have tracked floricans over three successive seasons (2008–2010), identifying non-breeding migration sites that should be prioritised for protection. Floricans from northern and southern breeding sites did not overlap in their use of non-breeding areas, requiring the protection of separate areas to serve each population. In the north there is poor overlap between protected areas and non-breeding sites used by tagged birds. For southern birds, there are no protected areas serving their non-breeding habitat. Northern birds travelled further but had smaller home ranges than southern birds, suggesting that their non-breeding habitat was better in quality but located at a greater distance. Movements proved facultative, with some birds remaining in breeding areas when conditions were sufficiently dry.

Introduction

The Bengal florican *Houbaropsis bengalensis* is Critically Endangered, with an estimated global population of fewer than 1,000 individuals, two-thirds of which are found in Cambodia (Gray et al., 2009). Therefore effective conservation of the Cambodian population is vital to the future persistence of this species. Previous research has focused on the breeding (dry season) areas, which in Cambodia consist of alluvial grasslands surrounding the Tonle Sap, South-East Asia's largest freshwater lake. Key dry season grassland sites have been identified, at least in terms of the distribution of male leks, and dry season habitat preferences have been investigated (Gray et al., 2007, 2009a, 2009b). In response to rapid conversion of the grasslands to intensive agriculture, Bengal Florican Conservation Areas (BFCAs) were established and now protect 173.3km^2 of breeding habitat (van Zalinge et al., 2010).

Clearly for a Critically Endangered species it is vital to discover the areas and habitats it occupies throughout the year in order to monitor and protect populations against potential threats. In the Cambodian wet season (May/June–November/December), the floricans' breeding grasslands in the floodplain are inundated, but until now very little was known of the movements and locations of the birds during this non-breeding period. Floricans had been reported from areas of open dry dipterocarp forest and grassland beyond the floodplain in the wet season (Seng Kim Hout et al., 2003; Davidson, 2004; Evans et al., 2009). These habitats are being encroached and converted by plantation concessions and expanding agriculture (Evans et al., 2009; van Zalinge et al., 2010). Therefore, two additional BFCAs were designated in September 2008, covering an area of 138.2km^2, encompassing the location of the majority of confirmed non-breeding records at that time, plus adjacent areas of potentially occupied habitat (but excluding large areas which had already been issued as concessions for agricultural plantations or included a high percentage of small-scale, privately owned agricultural plots). However, the lack of a comprehensive understanding of wet season movements and non-breeding sites risked failure to detect or counter threats to the species during this period.

Until now, locating floricans during the wet season has proved problematic. Much of the landscape is under water at this time of year, restricting access, and fewer people venture into the water-logged landscape, so incidental florican sightings are sparse. The species is particularly inconspicuous during the wet season, with the males mostly losing their bold black and white plumage, acquiring a more subtle mottled brown plumage, similar to that of the

highly cryptic female. The behaviour of both sexes becomes secretive (Son Virak pers. obs.), possibly in part owing to the hunting pressure to which birds are exposed (Collar, 2001). Most sightings of floricans during the wet season have involved accidental flushing at close range, from a position hidden in vegetation, in response to disturbance (Son Virak pers. obs.). Some attempt to understand non-breeding distribution was made by interviewing villagers and mapping localities where floricans were reported to be present (Davidson, 2004; Evans et al., 2009). However, although achieving wider geographic coverage, this method suffers from uncertain temporal quality – and it is not always clear whether reported presence indicates continued occupancy. More recently, field surveys have been undertaken, focusing on areas within the non-breeding season BFCAs and adjacent surrounding areas (van Zalinge et al., 2009, 2010). These are necessarily restricted in geographic scope as only a relatively limited area can be covered, leaving extensive areas of potential habitat uninvestigated. Survey results have been further hindered by low encounter rates.

Whilst floricans have been successfully radio-tracked during the breeding season (Gray et al., 2009), the potential for locating individuals in the wet season by radio telemetry is very limited, as they move beyond the detectable range of radio receivers into unknown areas. There is a strong bias towards detecting birds only at those locations that are accessible, previously known and are therefore searched, thus excluding unknown and inaccessible localities. In contrast, satellite telemetry enables florican movements to be tracked remotely over large areas and can provide unbiased information on non-breeding areas.

This is the first study to track floricans to non-breeding areas during the wet season. The aims were to gain understanding into florican movements, distribution, differences in landscape use between breeding areas and between males and females, along with the influence of seasonal factors on migratory patterns.

Methods

Study area

Satellite transmitters were deployed on floricans at five dry season sites in the south-eastern part of the Tonle Sap floodplain (Figure 1). These sites fall mostly within Kompong Thom Province, with the most northerly site extending into Siem Reap Province, and are drawn from the core area of the Cambodian florican population, estimated to hold around 75% of the Cambodian population in 2005 (Gray et al., 2009).

Satellite transmitter deployment

A total of 21 satellite transmitters were deployed at florican dry season sites during February–March 2008 (n = 3), 2009 (n = 7) and 2010 (n = 11) on 12 male and 9 female floricans. Floricans were captured by herding with a vehicle into 50–100m long nets (see Appendix). Units were backpack-style fitted with a Teflon tape harness, and comprised Microwave Telemetry 45g solar Argos/GPS (n = 5), Microwave Telemetry 35g solar Argos (n = 11) and North Star Science & Technology 30g battery Argos (n = 5). Mean weight of males was 1221g (range 1002–1426), and of females was 1340g (range 1177–1474). The highest transmitter to body weight ratio was 3.8% (below the 4% maximum recommended by Kenward, 2000). Locations received within the first 24 hours of an individual being fitted with a transmitter were discarded so as not to include in the analysis any atypical movements that might have resulted from capture experience.

Migratory *vs* sedentary status, wet season areas and wet season regions

In each wet season, a bird was classified as 'migratory' if it used an area during the wet season which had no overlap with its dry season home range, and as 'sedentary' if no such movement took place and its wet and dry season home ranges overlapped. 'Wet season areas' were determined for migratory individuals from location fixes received from areas occupied in the wet season following outward migration, until their return migration. For sedentary individuals, wet season locations and home ranges were determined from those locations that fell between the mean departure and return dates of migratory individuals in that year, calculated separately for males and females.

Birds captured at any of the three northern dry season study sites (Stoung-Chikreng BFCA, San Kor and Krous Kraom: Figure 1) were found to migrate to a distinct region in the northern part of the study area. In contrast, birds captured in the two southern dry season study sites (Chong Dong and Baray BFCAs: Figure 1) shared a wet season area which was separate from that of the northern birds (the shortest distance between wet season locations of northern and southern birds was 50km). Therefore, for the purpose of analysing timing, distance and duration of migration, these two groups are compared (hereafter referred to as 'northern' and 'southern' respectively).
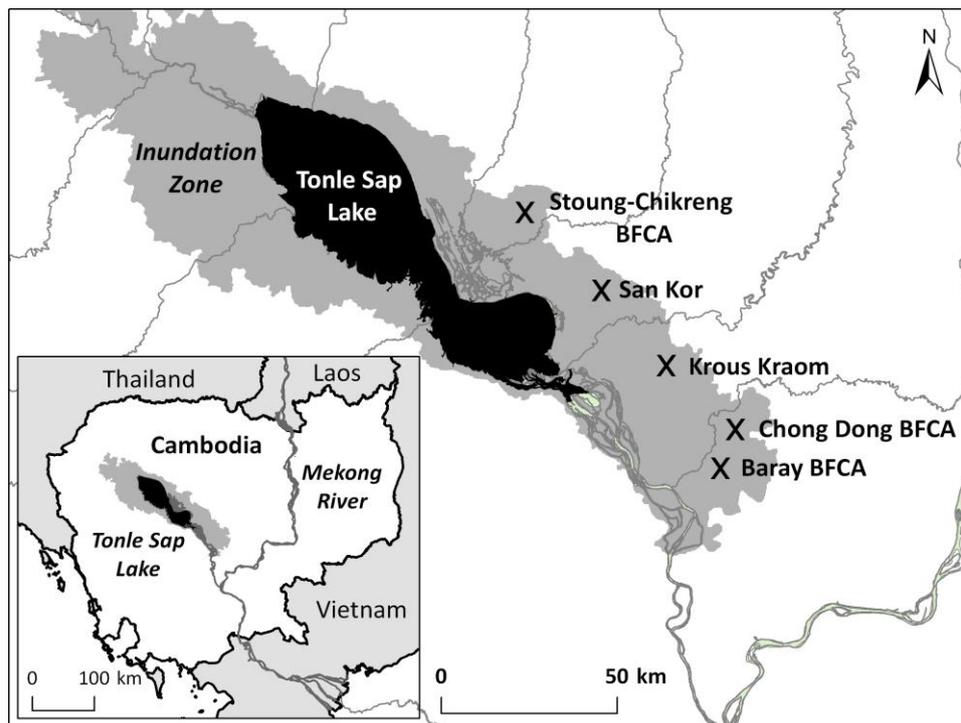
Figure 1. Location of dry season sites (X) where satellite transmitters were deployed on floricans, in the Tonle Sap floodplain, Cambodia. Black and grey shading show dry and wet season extent of the Tonle Sap Lake respectively.

Timing of wet season migrations

All migrations were included in the analysis, subject to the error reduction criteria outlined below, with multiple migration journeys observed for some individuals. The effect of pseudoreplication (by including two migrations from each of four individuals) was considered to be minimal in comparison to the effect of seasonal factors on timing of migration (with individuals making two migrations showing considerable inter-annual variation in departure and return dates).

GPS fixes (<100m error radius), along with Argos location classes 3 (<250m error), 2 (250–500m error) and 1 (500–1500m error), were used to determine the date of the last location in the dry season area and the first location following migration to the wet season area (and vice versa for the return journey). Argos errors (maximum 1.5km) were small relative to distances moved when migrating (over the order of tens of kilometres), so that inclusion of the lower-resolution class 1 fixes is justified, to increase accuracy of estimated time of departure. The duty cycles and performance of transmitters (frequency at which good quality locations were received) were such that the precise day of migration could only be specified for three (out of 18) departures and for none of the return journeys. Therefore the mid-point between last/first dates in dry/wet season areas was used as an estimate of the day of departure to and day of return from the wet season area. To reduce the error in departure/return date analysis, only those individuals with a gap between the last dry season area location and the first migratory wet season location of 13 days or less (based on 50% of the standard deviation in departure dates for the full data) were considered in the analysis of timing, resulting in a potential maximum error from the mid-point assumption of 6.5 days. This allowed 17 out of 18 migrations to be included in the departure date analysis; and for the return migration it reduced the sample size to 11 out of 17 migrations (for one individual tracked through the wet season, transmissions ceased at the onset of the dry season, prior to the return migration). For the estimate of the duration of wet season area occupancy, only those individuals with a total error gap of 20 days or fewer (from the combined estimation of both outward and return journey dates) were included in the analysis. This resulted in a sample size of 11 (out of a total of 17 migrations). The number of the day in the year, from 1 January (day 1) to 31 December (day 365), is used in figures and analyses.

Wet season site fidelity and migration distances

For the purposes of examining site fidelity and migration distances, only those location data obtained from GPS (13% of fixes) and Argos location classes 3 (37%) and 2 (50%) fixes were used, such that maximum error is <500m. Latitude and longitude location fixes were converted to Universal Transverse Mercator (UTM) to give true distances between locations. Wet season site fidelity of the four individuals observed over more than one wet season was assessed by two measures, used as basic measures of site fidelity. First, the average wet season location for each year of migration of each individual was calculated and the distance between them measured. Second, Minimum Convex Polygons (MCPs) were generated using Hawth's Tools

extension (Beyer, 2004) in ArcGIS 9.2 (ESRI, 2006) for each wet season, and the percentage of the area of the first season's home range that was overlapped by the second season's home range was calculated. Home range kernels (overlap or distance between centroids) were not used owing to the small number of locations for some individuals in certain years.

Distances travelled by migratory individuals were measured as the distance between the mean dry season location and mean location in the subsequent wet season. For individuals with multi-season data, the mean distance travelled (considering all years in which the individual migrated) was used as they exhibited strong site fidelity; differences in distances travelled between years were minimal (mean difference between years was 1.9km, *SE* = 1.0, n = 4).

Wet season home ranges

Autocorrelation between location fixes is a common issue when calculating home ranges (Swihart and Slade, 1985; Seaman and Powell, 1996). However, testing for this (Schoener, 1981; Swihart and Slade, 1985) and removing locations to avoid autocorrelation often results in discarding so many fixes that the remaining sample size may no longer be sufficient for home range analysis. Autocorrelation is increasingly thought not to be a major issue (Fieberg, 2007), and adequately sampling locations throughout the study is considered more important than determining statistical independence between locations (McNay et al., 1994). As a compromise and to retain sufficient sample sizes, locations obtained less than 15 minutes apart were discarded to remove highly autocorrelated fixes. Fifteen minutes was chosen as the amount of time within which a florican could easily cross its home range. As some bandwidth calculation methods for kernel analysis (e.g. least squares cross-validation and biased cross-validation) cannot be performed on duplicate locations, identical location coordinates were shifted a short distance, to retain the information of a high use area but avoiding the problem of duplicate location coordinates (Rodgers and Kie, 2011).

With the exception of the site fidelity analysis, home ranges were examined by probability density kernels; these are now widely used in preference to Minimum Convex Polygons that reveal no information on intensity of use within the home range, are strongly influenced by outer fixes, and are more strongly affected by autocorrelation (Swihart and Slade, 1997; Kenward, 2000; Laver and Kelly, 2008; Kie et al., 2010). Wet season home range kernels were produced for the ten individuals with at least 24 location fixes of GPS, or Argos Location

Classes 3 and 2 accuracy, for which the mean number of locations was 64 (SD = 38.3, range 24–127, n = 10).

Home range kernels can be fixed (same level of smoothing applied to all of an individual's locations) or adaptive (smoothing level can vary so that areas with a low density of locations receive greater smoothing than areas with a high density of locations: Worton, 1989). Although fixed kernels may accurately represent probability density distributions of many datasets (Worton, 1995; Seaman and Powell, 1996; Seaman et al., 1999), they perform poorly when outer areas contain a low density of fixes (Rodgers and Kie, 2011). Adaptive kernels have been found to perform well for some location distributions (Worton, 1989); the choice of method may best be decided by exploring the data (Rodgers and Kie, 2011). For our location distributions, characterised by multimodal clumps with outlying points, fixed kernels had a tendency to produce islands around individual outlying points, 'under-smoothing', while adaptive kernels provided a better fit. Adaptive kernels are often criticised for over-smoothing (Rodgers and Kie, 2011), but with our data they appeared to respond better to outlying points by not including them in the home range (which seemed appropriate as such points are unlikely to be truly a part of the regular use area and are probably exploratory in nature). Figure 2 provides an example of differences in home ranges produced by fixed and adaptive kernels for a florican's wet season locations.

Selection of the appropriate bandwidth is considered far more important than the choice between fixed or adaptive kernels (Worton, 1995; Seaman and Powell, 1996, Figure 2). The reference bandwidth (href) can be satisfactory for unimodal data (Silverman, 1986), but otherwise often greatly over-smoothes multimodal data, leading to gross over-estimation of home range extent, as was the case with our data (Figure 2 B & E), and therefore is not recommended for multimodal density distributions (Seaman et al., 1999).

Least squares cross-validation (LSCV) is a popular method of bandwidth selection (Seaman et al., 1999; Laver and Kelly, 2008) but, as found by others (Park and Marron, 1990; Sain et al., 1994), produced excessive under-smoothing, with the outer 95% isopleth highly fragmented into multiple small isolated islands (Figure 2 A & D). Biased cross-validations (BCV) was also inappropriate for our data as, like LSCV, it cannot be computed for distributions with clustering of many locations that are very close together (Rodgers and Kie, 2011).

An ad-hoc approach to determine the smallest proportion (sequentially reduced by 0.05 decrements) of the href value that maintains an intact outer contour (95% isopleth) minimises both over- and under-smoothing and is increasingly widely adopted (Berger and Gese, 2007; Jacques et al., 2009; Kie et al., 2010; Rodgers and Kie, 2011). However, this was not suitable as individual Bengal floricans often occupied several disjunct areas during different periods of the wet season, with extensive unoccupied areas in-between; restricting bandwidth to maintain an uninterrupted outer contour included these large unutilised areas within the home range, resulting in substantial over-smoothing (equivalent to Figure 2 E).

Finally a set proportion of the href value can be applied to all individuals (Bertrand et al., 1996; Kie and Boroski, 1996; Kie et al., 2002, 2010). Whilst selection of the proportion value is somewhat arbitrary, this was based on a thorough exploration of the data and averaging the proportional values considered most appropriate for each individual's distribution from visual inspection. This resulted in the use of a fixed 0.3 of the href value, which gave satisfactory results for all individuals (Figure 2 F) and seemed the best method given the nature of our data and the difficulties explained above.

Home range kernels were produced from locations in UTM format in ArcGIS 9.2 using HRT: Home Range Tools for ArcGIS (Rodgers et al., 2007). A raster cell size of 30x30m, whilst slower to compute than for larger cell sizes, was selected as compatible with LANDSAT imagery cell size for subsequent habitat analysis (Chapter 4). Isopleths of 50% (core area) and 95% (home range) were generated.
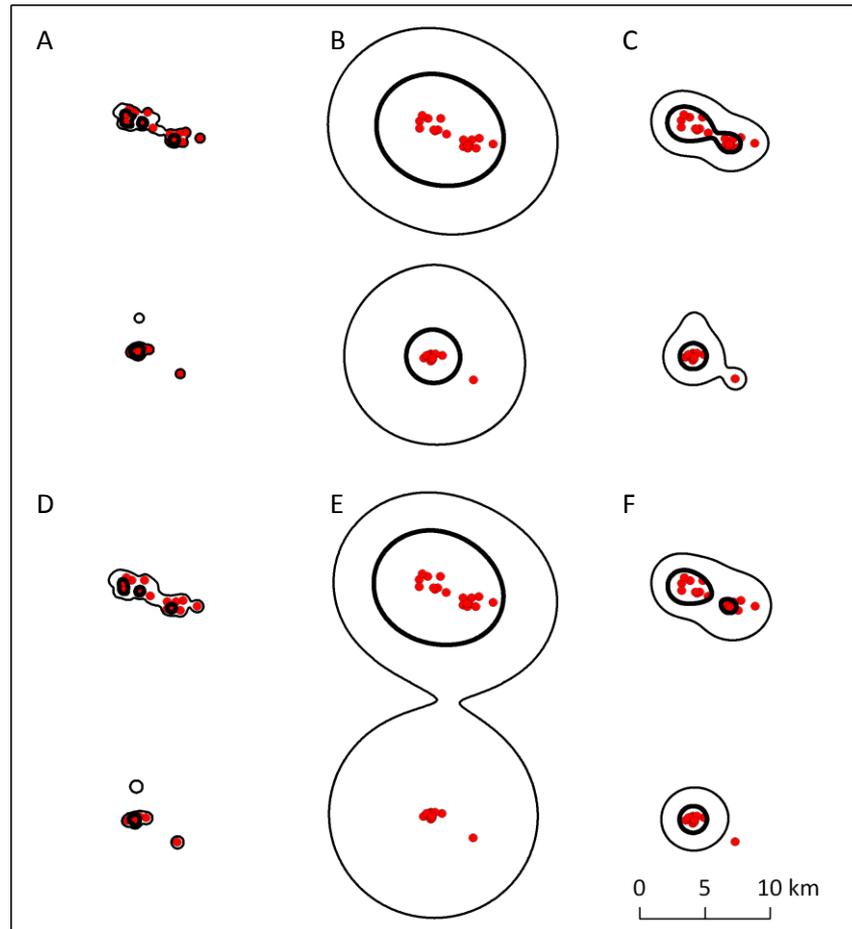
Figure 2. The effect of LSCV (A, D), href (B, E) and 0.3 x href (C, F) smoothing parameters on the construction of a florican's wet season home range kernel (location points shown as red dots), displaying the outer 95% contour (thin line) and inner 50% core area (thick line). A, B & C were produced using fixed kernels, while D, E, & F used adaptive kernels.

Survival analysis

Monthly survival estimates were calculated from tracking data, following Mayfield (1961, 1975, adapted for survival analysis; Trent and Rongstad, 1974), with confidence intervals calculated from estimated standard error following Johnson (1979). For radio-tagged birds that disappeared, the number of months monitored was estimated following the mid-point interval assumption.

Monthly mortality rates were calculated from the number of individuals that went missing (prior to expected transmitter failure) or that were confirmed dead; as this may include some

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individuals for which transmitters failed, this represents a maximum mortality rate. Minimum monthly survival estimates ($\hat{S}_m$) were calculated as:

$$\hat{S}_m = 1 - (\text{number of deaths} / \text{number of months monitored})$$

The frequency of hunting reports in the years 2009–2011 was also assessed by month, to compare dry and wet season hunting pressure.

Statistical analysis

Data were checked for normality (by visual inspection of frequency histograms) and equal variance (by Levene's Test for Equality of Variances). Differences in the timing of migration were compared between 2009 and 2010 (2008 was excluded owing to small sample size) with t-tests. The effects of region (northern/southern) and sex on timing of migration, distances moved and home range sizes were assessed with General Linear Models (two-way Analysis of Variance, omitting interaction terms for which no a priori hypothesis existed). Home range size raw data did not meet parametric assumptions; this was rectified using a log transformation. Traditionally, inflation of Type I error rates (i.e. the probability of falsely declaring a result significant) when conducting multiple statistical tests has been controlled by constraining probability thresholds to an experiment-wide error rate, through Bonferroni correction (Rice, 1989). However, this procedure reduces statistical power and substantially increases the likelihood of Type II error (i.e. the probability of failing to detect a genuine difference) (Nakagawa, 2004). Therefore, where two tests were performed on the same data (as for timing aspects), effect sizes are referred to in preference to Bonferroni correction, as recommended by Nakagawa (2004). Effects sizes were calculated for t-tests as:

$$r = \sqrt{(t^2 / (t^2 + df))}$$

For General Linear Models, effects sizes were calculated as the square root of the partial eta squared (η^2), where SS is the sum of squares:

$$\text{Partial } \eta^2 = SS_{Factor} / (SS_{Factor} + SS_{Residual})$$

Effect sizes are reported following Cohen's (1988) thresholds of: $r = 0.10$ small effect, $r = 0.30$ medium effect, $r = 0.50$ large effect. Percentage of variation explained by factors are presented

as r^2 (x 100). Statistical analyses were carried out using SPSS 16.0. Fisher's Exact test was used to assess differences in the proportion of males/females and northern/southern birds undertaking migration in 2010.

Results

Wet season migration/residency patterns

In both 2008 (*n* = 3) and 2009 (*n* = 9) all tagged floricans migrated to wet season areas that were distinct from their dry season (breeding) areas, whereas in 2010 only six out of 15 floricans migrated, with nine (60%) remaining in their dry season home ranges throughout the wet season (Figure 3). The decision to migrate was clearly facultative and not a fixed trait; of five individuals tracked for more than one year, four failed to migrate in 2010 despite having shown migratory behaviour in previous years (Figure 3). In 2010, there was no significant difference in migration/residency between males and females (Fisher's Exact, *p* = 1.00); similarly, although half of the southern birds (3/6) compared to just a third of the northern birds (3/9) migrated, this apparent difference was not significant (Fisher's Exact, *p* = 0.62).
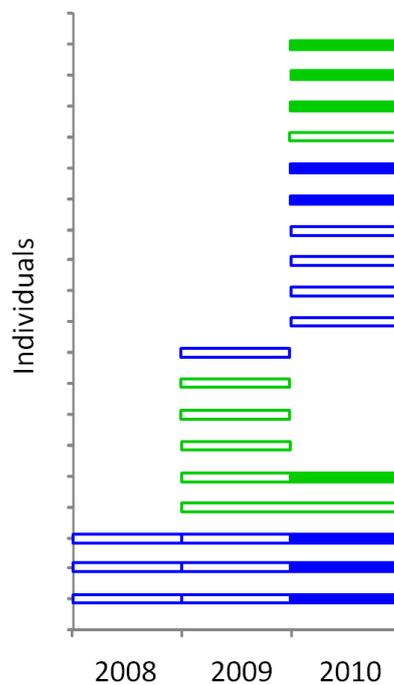
Figure 3. Annual patterns of wet season migratory (hollow bar) and sedentary (solid bar) behaviour for each tagged male (blue) and female (green), 2008–2010. Four of the transmitters deployed in 2009 were battery-powered units lasting one year only.

Wet season migration sites

Fourteen floricans from five breeding sites were tracked during the wet season to non-breeding migratory areas beyond the floodplain, between 2008 and 2010 (Figure 4). Floricans from the three northern breeding sites utilised the same broad non-breeding area, separate from those of the southern birds. Individuals from within each region spread quite widely across the landscape, relative to their breeding ranges.

Timing of wet season migration

Effects of inter-annual variation in flood level and rainfall on timing of migration

There was a marginally significant trend for earlier departure in 2009 than in 2010 (t_{12} = −1.82, p = 0.093), which represented a medium-sized effect, r = 0.466 (Table 1). Mean departure date for 2008 fell between that for 2009 and 2010 but was not included in these comparisons owing to the small sample size. This variation in departure dates is likely to be related to cumulative rainfall, which was greatest during 2009, such that flood levels rose earlier and achieved the greatest depths in that year, with the driest conditions in 2010 and intermediate conditions in 2008 (Figure 5). Mean return date was similar in 2010 and 2009 (t_8 = −0.973, p = 0.359, r = 0.326). Duration of stay in the non-breeding area was longer in 2009 than 2010; although not significant, t_8 = 1.22, p = 0.256, the effect was medium-sized, r = 0.397.
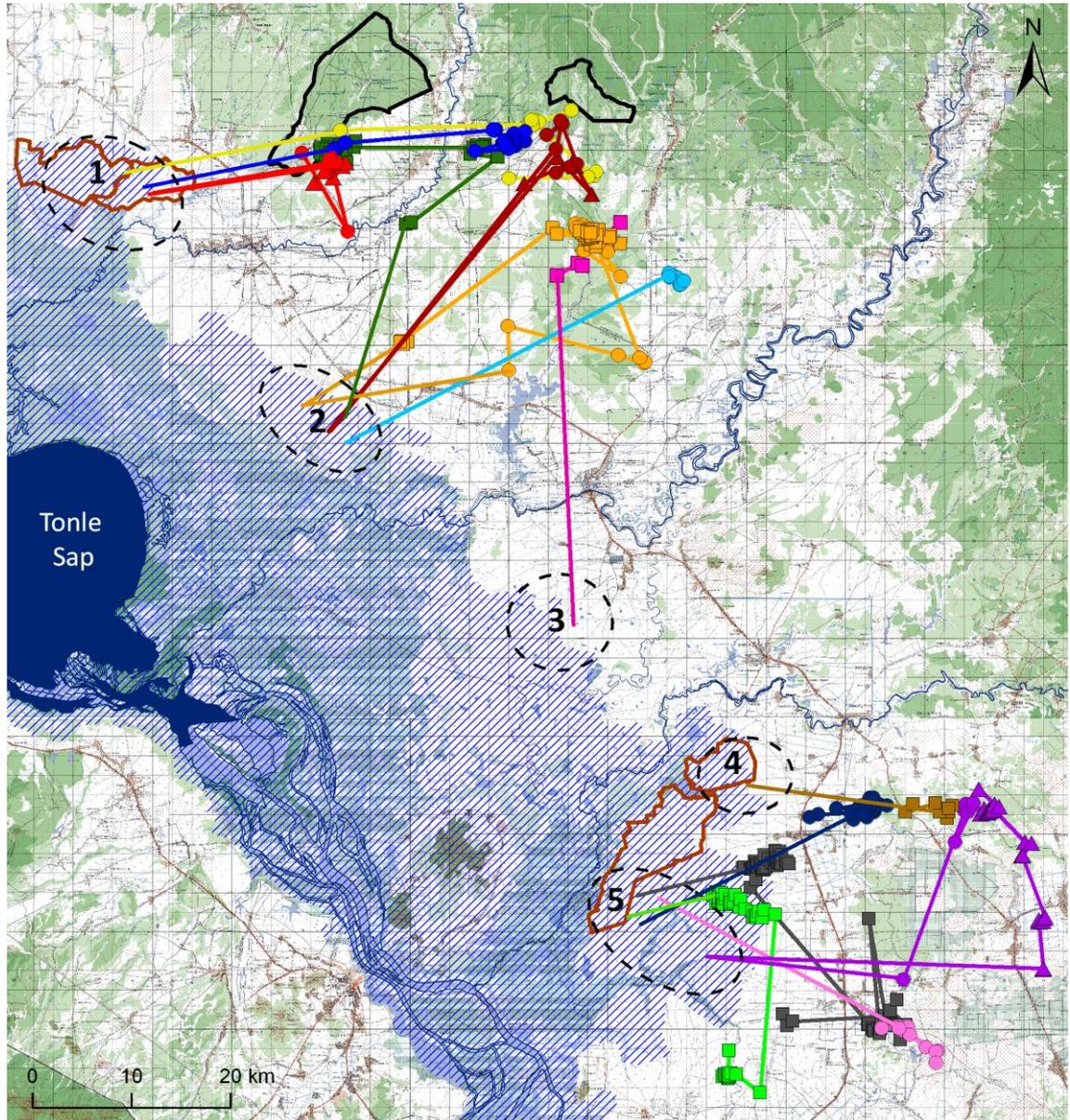
Figure 4. Wet season migration of 14 individuals (separated by colour) showing locations in 2008 (△), 2009 (○) and 2010 (□) with paths linking consecutive locations (solid lines) for each wet season migration, starting (only outward paths shown) from a individual's core area of the dry season site (circled with a dashed line: 1 Stoung-Chikreng, 2 San Kor, 3 Krous Kraom, 4 Chong Dong and 5 Baray). Breeding (brown) and non-breeding (black) BFCAs are outlined. The dry season (solid blue) and maximum wet season (hatched blue) extent of the Tonle Sap lake is shown. Map elements are overlain on a topographic map.

Table 1. Mean Julian Day (and Calendar Date) of departure to and return from wet season areas and mean length of time of wet season occupancy (with standard errors and sample sizes) for 2008, 2009 and 2010. Return date and duration in wet season area for 2008 are based on a single bird only.

Year	Departure date			Return date			Duration (number of days)		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
2008	243 (31 Aug)	12.2	3	336 (2 Dec)	n/a	1	69	n/a	1
2009	232 (20 Aug)	5.5	8	341 (7 Dec)	8.6	5	106	14.6	5
2010	259 (16 Sept)	15.4	6	354 (20 Dec)	9.7	5	82	13.0	5
All	**243 (31 Aug)**	**6.7**	**17**	**347 (12 Dec)**	**5.9**	**11**	**92**	**9.4**	**11**
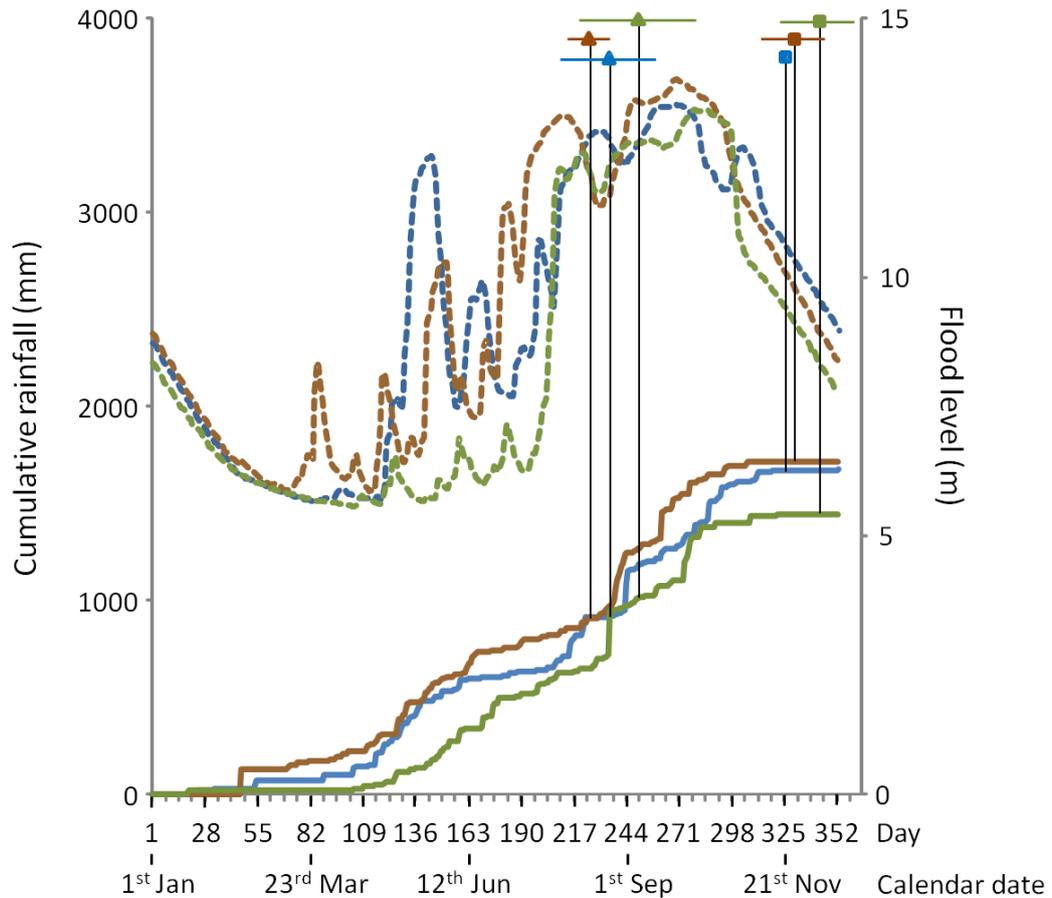
Figure 5. Mean date (± 2 SE bars) of departure to (▲) and return from (■) non-breeding grounds in relation to cumulative rainfall (solid lines) and flood level of the Tonle Sap (dashed lines) for 2008 (blue), 2009 (brown) and 2010 (green). Dates for 2008 departure and return are based on only three birds and one bird respectively and are included as an indication only.

Effect of region and sex on timing of migration

Departure date did not differ between regions ($F_{1,14}$ = 0.112, p = 0.742, r = 0.089) or sexes ($F_{1,14}$ = 0.025, p = 0.876, r = 0.045; Figure 6). Mean return dates were earlier for southern than northern sites (Figure 6A), and although this was not significant ($F_{1,8}$ = 2.340, p = 0.165) it represented a medium-sized effect (r = 0.475). Return dates for males and females were similar ($F_{1,18}$ = 0.040, p = 0.847, r = 0.071, Figure 6B). However, females spent marginally longer (approaching the significance threshold) in wet season areas than males ($F_{1,8}$ = 4.120, p = 0.077), with a large effect size (r = 0.583). Time spent in wet season areas did not differ between northern and southern birds ($F_{1,8}$ = 0.090, p = 0.771, r = 0.332). Timing of movements is shown separately for northern and southern males and females in Table 2.
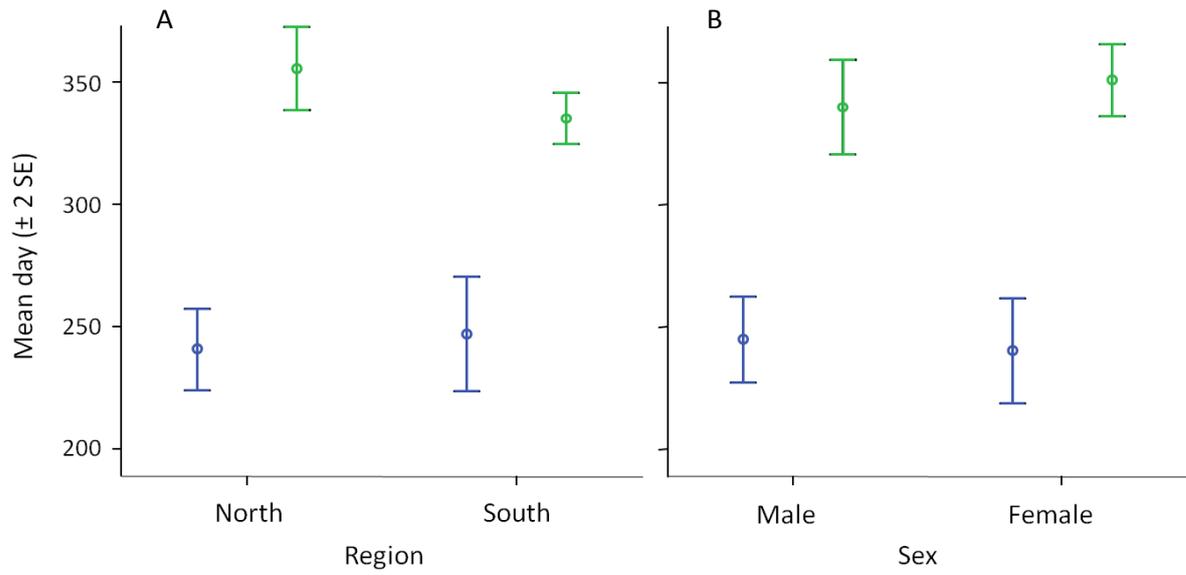
Figure 6. Mean (± 2 *SE* bars) day for departure to (blue) and return from (green) wet season migration areas by (A) region and (B) sex.

Table 2. Mean Julian Day (and Calendar Date) of departure to and return from wet season areas and mean length of time individuals spent in wet season area (with standard errors and sample sizes) for northern and southern males and females.

Region	Sex	Departure date			Return date			Duration (no. of days)		
		$\overline{x}$	SE	n	$\overline{x}$	SE	n	$\overline{x}$	SE	n
North	Male	239 (27 Aug)	12.1	5	377 (12 Jan)	n/a	1	91	n/a	1
	Female	243 (31st Aug)	12.9	5	351 (17 Dec)	9.0	5	108	12.2	5
South	Male	250 (7 Sept)	13.2	6	331 (27 Nov)	4.1	4	63	9.2	4
	Female	228 (16 Aug)	n/a	1	354 (20 Dec)	n/a	1	124	n/a	1
Total All				17			11			11

Distances travelled to wet season migration areas and inter-annual site fidelity

Multi-annual data were obtained for only five individuals, of which four provided observations of migration in more than one wet season. These individuals returned to similar wet season areas in each year of migration (Table 3, Figure 4). Only one (a subadult male) did not have any overlap in MCPs between years; however, for this individual the second season MCP was based on only seven fixes (and is therefore unlikely to be very representative) and the distance between mean locations in each year was relatively small (5.2 km).

For those floricans that migrated, northern birds travelled significantly further ($\bar{x}$ = 33.8 km, *SE* 2.6, *n* = 8) than southern birds ($\bar{x}$ = 22.1 km, *SE* = 3.0, *n* = 6: $F_{1,11}$ = 7.509, *p* = 0.019), with a large effect size (*r* = 0.673). The distance travelled by males ($\bar{x}$ = 25.5, SE = 3.4, n = 8) and females ($\bar{x}$ = 33.1, SE = 2.8, n = 6) did not differ ($F_{1,11}$ = 0.934, *p* = 0.355, r = 0.279). Mean distances travelled separated by both region and sex are shown in Table 4.

Table 3. Wet season site fidelity for four individuals tracked migrating in two wet seasons, expressed in terms of the distance between mean wet season locations and percentage of Minimum Convex Polygon overlap between years. MCPs were based on a mean of 24 (range 4–90) fixes.

Sex	Region	Distance (km)	% MCP overlap
Female (subadult)	Northern	0.4	8.7
Male	Northern	0.9	67.7
Male	Northern	2.9	14.7
Male (subadult)	Southern	5.2	0.0
Mean (n=4)		**2.4 (*SE* = 1.1)**	**23 (*SE* = 15.3)**

Table 4. Mean distances travelled on migration between dry and wet season areas (with standard error and samples sizes) for northern and southern males and females.

Region	Sex	Distance (km)		
		$\bar{x}$	*SD*	*n*
North	Male	32.3	9.8	3
	Female	34.7	6.4	5
South	Male	21.4	7.9	5
	Female	25.3	n/a	1
Total				14

Wet season home ranges of migratory and sedentary individuals

Wet season home range kernels (with 50% and 95% isopleths) for ten Bengal floricans (all those with at least 24 locations for the wet season period) are shown in Figure 7. For eight of these 10 individuals, home ranges overlapped with that of at least one other satellite-tracked individual. Two females (with home ranges shown in orange and red in Figure 7A) were non-migratory, occupying their dry season home ranges throughout the wet season. The home ranges for these two individuals fell almost entirely within the boundary of the dry season BFCA. Of the eight migratory individuals shown, the wet season home ranges of only two (northern) overlap with a BFCA, both utilising the same area of the BFCA and only for part of the wet season; all other individuals migrated to areas that were unprotected.

All wet season home ranges were multimodal. Floricans from southern sites had larger (marginally significant) wet season home range cores (50% isopleths: $\bar{x}$ = 7.8 km^2, *SE* = 2.4, *n* = 4) than those from northern sites ($\bar{x}$ = 1.8 km^2, *SE* = 0.4, *n* = 6: $F_{1,7}$ = 5.333, *p* = 0.054), with a large effect size (*r* = 0.657); however, 50% core home range did not differ between males ($\bar{x}$ = 7.4 km^2, *SE* = 2.7, n = 4) and females ($\bar{x}$ = 2.0km^2, *SE* = 0.4, n = 6: $F_{1,7}$= 0.036, *p* = 0.855, *r* = 0.071). Mean home range kernels, measured as 95% isopleths, were also on average larger for southern ($\bar{x}$ = 72.1 km^2, *SE* = 26.3, *n* = 4) than northern sites ($\bar{x}$ = 29.0 km^2, *SE* = 13.5, *n* = 6), although non-significant ($F_{1,7}$= 0.775, *p* = 0.408, *r* = 0.316). There was no significant difference in mean 95% isopleth areas for males ($\bar{x}$ = 71.5km^2, *SE* = 26.8, *n* = 4) and females ($\bar{x}$ = 29.4 km^2, *SE* = 13.4, n = 6; $F_{1,7}$= 0.336, *p* = 0.580, *r* = 0.215). Mean home range sizes separated by both region and sex are shown in Table 5.
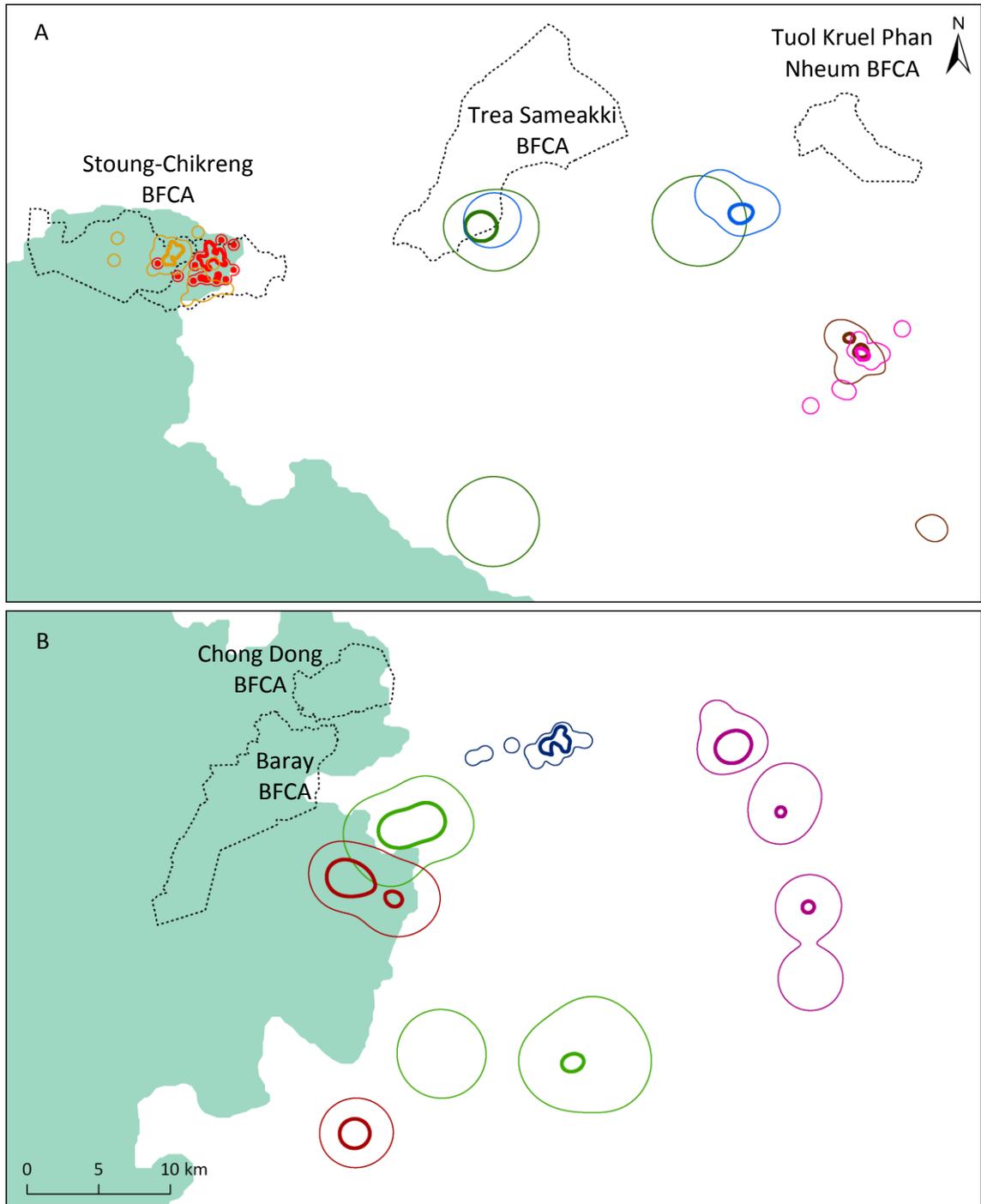
Figure 7. Wet season home ranges (from a single season) for ten Bengal floricans from northern (A) and southern (B) sites. Home ranges of individuals are shown in different colours. Thick contour lines represent inner 50% isopleths, thin lines represent outer 95% isopleths. The two most westerly home ranges (in orange and red) of A were for non-migratory individuals. Dashed black lines show perimeters of BFCAs. Blue shading shows the maximum wet season extent of the Tonle Sap lake.

Table 5. Mean 50% and 95% home range areas (with standard error and samples sizes) for northern and southern males and females.

Region	Sex	50% home range		95% home range		
		$\bar{x}$	SE	$\bar{x}$	SE	n
North	Male	0.6	n/a	8.7	n/a	1
	Female	2.0	0.4	33.0	15.8	5
South	Male	9.6	2.1	92.4	53.4	3
	Female	2.1	n/a	11.1	n/a	1
Total						10

Survival analysis

Twenty-one individuals were monitored by satellite transmitters, over a total of 416 months (Figure 8). Three likely mortality events were detected, consisting of two cases where fixes ceased and one case of confirmed death due to hunting. The estimated Monthly Survival Rate ($\hat{S}_m$) was 0.9928 (95% CI: 0.9847–1.00), resulting in an estimated mean annual survival of 0.917 (95% CI: 0.831–1.00). When additional information from nine radio-tagged individuals (see Figure 8), for which temporal resolution was poorer, is also included the resulting estimated mean monthly survival rate based on the overall total of five observed disappearances (from a total of 30 individuals) over 609 monitored months, was 0.9918 (95% CI: 0.9846–0.9990), resulting in a mean annual survival rate of 0.906 (95% CI: 0.830–0.988).

Seasonal analysis was undertaken solely for the 21 satellite-tagged birds, as there was uncertainty as to the seasonal timing of disappearance of two radio-tagged birds (Figure 8). No disappearance or mortality was observed for the dry season (across 250 monitored months). For the wet season, three disappearances were observed over 166 months, resulting in an estimated monthly survival rate over the wet season of 0.9819 (CI: 0.9616–1.00). Together, these suggest an overall annual survival rate of 0.896 (0.791–1.00).

For the three satellite-tagged birds that went missing/died, the two males were in breeding areas (at the onset of the wet season) and the female was in a non-breeding migratory area (at the end of the wet season). All hunting incidents reported between 2009 and 2011 were from the wet season, with seven occurring in breeding areas and two in non-breeding areas (Figure 9).
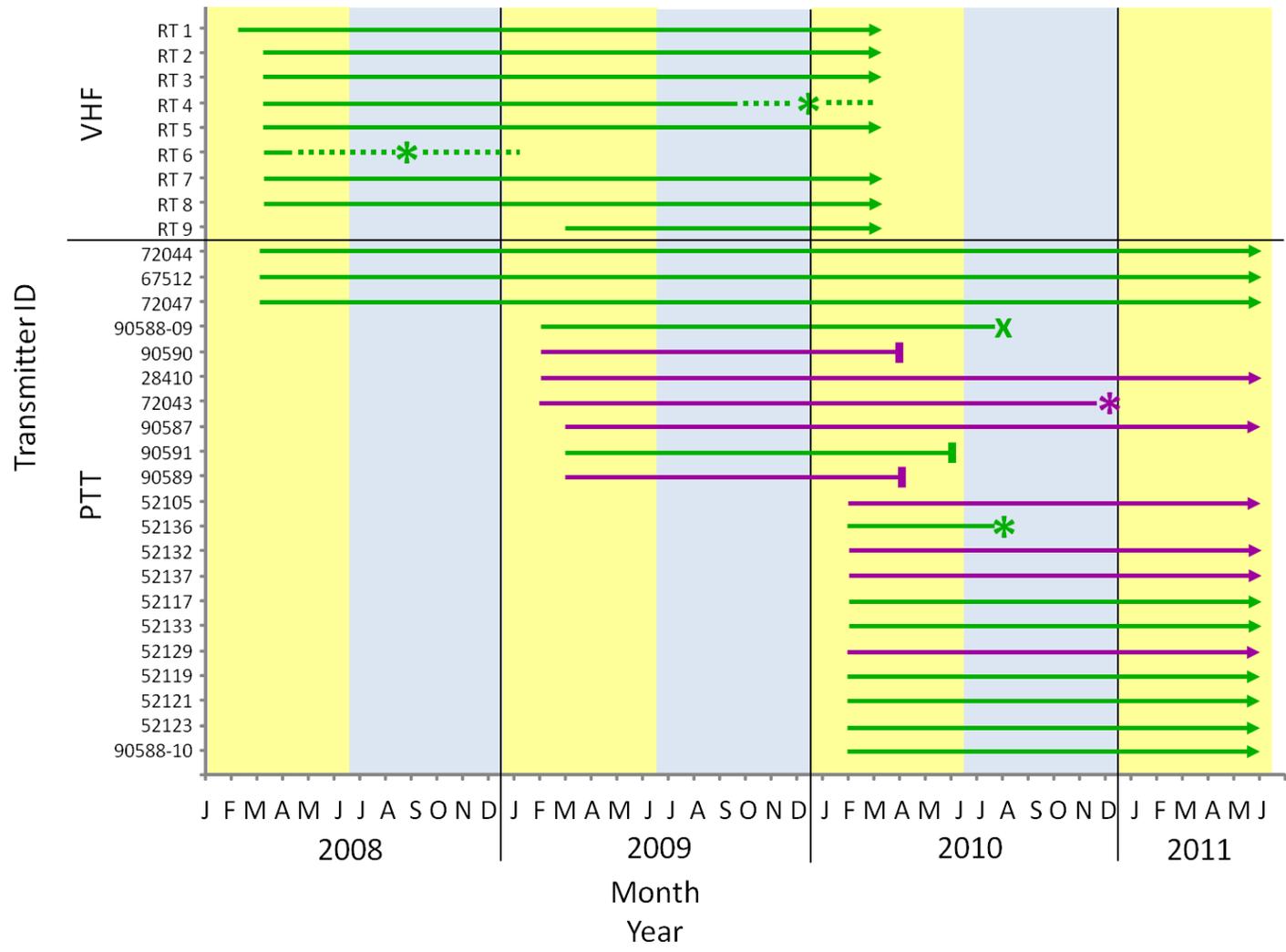
Figure 8. Survival outcomes for 30 Bengal floricans tracked by radio (VHF) or satellite (PTT) tags during 2008–2011. Solid lines show known duration alive, and end when no further data were collected (►), the transmitter battery was drained (for one year duration PTT units, ▌), the individual went missing (no more satellite fixes were received, prior to expected battery drain or unit failure, or could not be located by radio-tracking, ✳), or the bird was confirmed dead (**X**). Dashed lines with ✳ at their mid-point (for radio-tagged birds only) indicate uncertainty between the last month confirmed alive and subsequent tracking session when found to be missing (radio-tagged birds were only regularly monitored during the dry season). Survival information is shown for males (green) and females (purple). Dry and wet seasons are indicated by yellow and blue backgrounds respectively for each year.
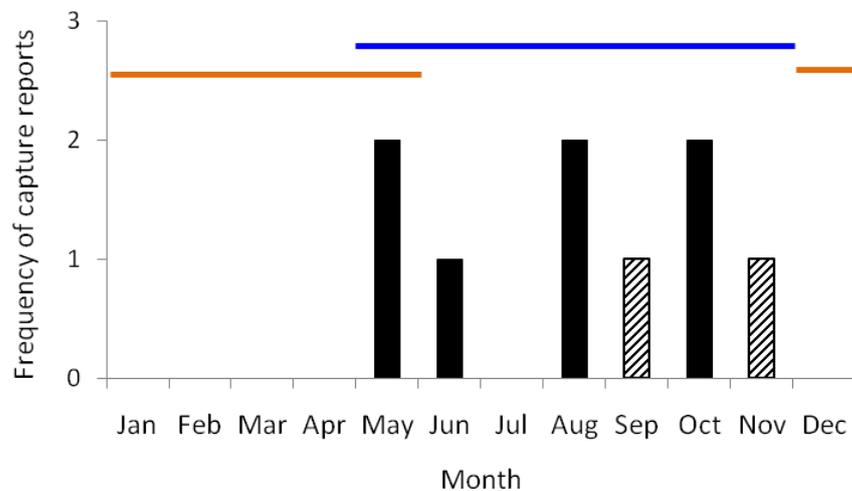
Figure 9. Frequency of reports of illegal florican captures by month for 2009–July 2011 (total = 9, of which four were adult males, four were adult females and one was a juvenile female c. 6 weeks old) with solid bars representing hunting captures from breeding areas and hatched bars those from non-breeding (migration) areas. Approximate dry (orange bar) and wet (blue bar) seasons are shown.

Discussion

Using satellite-tracking we have substantially improved understanding of florican migration and locations during the wet season in Cambodia. Wet season areas were located for individuals from five key breeding sites.

Annual migrations related to flood conditions

The satellite-tracking data suggest that this population exhibits 'facultative partial migration' during the wet season, where an individual may choose whether or not to migrate each season depending on environmental conditions (Terrill and Able, 1988). During 2010 nine out of fifteen birds remained resident on the breeding grounds throughout the wet season, during conditions that were drier, with lower flood levels and rainfall, than in 2008 and 2009. Migration is likely to be energetically costly and therefore, if the grasslands are not extensively flooded in a dry year, remaining resident may be a preferable strategy. Floricans undertaking migration spent just over three months in wet season areas. Annual migration patterns appeared to be linked to flood and rainfall levels. In 2009, the year with wettest conditions, birds departed from the breeding grounds on average 27 days earlier than in 2010. Partial migration in response to environmental conditions has also been observed in great bustards *Otis tarda*, where a variable number of males migrate to escape high summer temperatures in Spain (Alonso et al., 2009) and to avoid low winter temperatures in Central Europe (Streich et al., 2006).

Migration patterns between regions and sexes

It was hard to distinguish regional differences in migratory behaviour (timing, duration, wet season home range size) from possible sex-related differences, as most analyses of individuals with an adequate number of fixes were compounded by the large proportion of males from southern sites and females from northern sites. However, the effect of sex on duration of time spent in non-breeding areas (accounting for 34% of the variance) was much stronger than that of region (11% of the variance), with females spending longer in wet season areas than males. Males are likely to obtain better territories if arriving early on the breeding grounds and can exploit early/late season mating opportunities. Earlier return migration of males to the breeding grounds from non-breeding areas has been recorded in great bustards (Palacín et al., 2009) and many other bird species, particularly those for which such behaviour helps to ensure they obtain a good breeding territory (Myers, 1981; Kokko, 1999).

The southern breeding season sites tend to flood more deeply and for longer duration, so it would be expected that more birds from the southern sites would need to migrate. Accordingly, half of the southern birds migrated in the dry year of 2010, compared to a third of the northern birds. Alonso et al. (2009) reported regional differences in numbers of male great

bustards migrating and distances travelled, in keeping with variation between regions in the severity of environmental conditions they were seeking to avoid. Floricans from northern dry season sites travelled more than 50% further to reach wet season areas (with region accounting for 47% of the variance in distance travelled). This may be an additional contributing factor in the larger proportion of birds from the north remaining resident in 2010, as energetic demands and risks may be higher during longer migration.

Birds from the southern dry season breeding sites returned to the breeding grounds on average 24 days earlier than northern birds. With southern wet season areas lying in closer proximity to the breeding areas, birds from this region may experience conditions more like those on the breeding grounds and therefore obtain good indications of when conditions on the breeding grounds are sufficiently dry to return. Northern birds, by comparison, would have fewer clues to the conditions on the breeding grounds, and returning too early when sites are still flooded could put them at risk.

Core (50% isopleth) florican home range areas were larger in southern sites ($\bar{x}$ 7.8km^2) than in northern ones ($\bar{x}$ 1.8km^2). A similar pattern was shown for the 95% isopleths, but there was considerable variation among birds from both regions, probably owing in part to the influence of outlying points. The greater ranging and mobility of birds from southern sites seem likely to reflect less suitable habitat and resources. Home ranges were mostly multimodal, but individuals tracked over multiple years exhibited considerable inter-annual site fidelity to non-breeding season areas, as has been observed in some populations of great bustard (Alonso et al., 2000; Morales et al., 2000; Palacín et al., 2009) and houbara bustard *Chlamydotis (undulata) macqueenii* (Judas et al., 2006). Such site-faithfulness may limit the ability of adults with an established pattern of migration to adapt to habitat loss at traditional sites. In contrast, the two subadults tracked appeared to show greater exploratory ranging in their wet season migration.

Floricans from northern and southern dry season sites utilised disjunct wet season areas, with no instances of any individual migrating to sites used by birds from the other breeding subpopulation. Therefore, separate consideration will need to be given to wet season sites that serve northern and southern regions. Floricans also exhibit strong site fidelity to their breeding grounds, as evidenced by inter-annual fidelity of radio-tracked floricans (Gray et al., 2009). As discussed by Hingrat et al. (2004) and Combreau et al. (2011) in relation to houbara, this has considerable implications for population management units, as the ability to colonise

new areas, and indeed the opportunities for mixing of genetic material between sites, may be dependent on juvenile dispersal, on which we currently have no information.

Conservation implications

The identification of areas used by floricans during the wet season has been an essential step in the conservation of this vulnerable and beleaguered population, and will now allow the prioritisation of sites for wet season protection. In a region where habitat conversion is occurring rapidly, the loss of suitable wet season areas is likely to be a serious threat. Current BFCAs were little used by tagged floricans in the wet season, although field surveys by the Wildlife Conservation Society have produced a small number of records of floricans further into Trea Sameakki BFCA (van Zalinge et al., 2009, 2010). However, the boundaries of Tuol Kruel Phan Nheum BFCA (in which neither tagged birds nor field surveys have been able to confirm use by florican) should be reconsidered, also taking into account wet season habitat requirements (see Chapter 4). Protected sites in the northern region are likely to benefit a number of bird species, as much of this region has been designated as an Important Bird Area (Seng Kim Hout et al., 2003). At present, there is no provision for wet season sites used by southern floricans, which do not share the wet season areas of northern birds.

Hunting of floricans is likely to continue to pose a serious threat to the population, and the cases reported probably represent just a fraction of the actual number of hunting incidents. The risk appears to be highest during the wet season, when floricans are forced into closer proximity with people as floodwaters expand, and in breeding rather than non-breeding migration areas (Figures 8 & 9). This suggests sedentary behaviour during the wet season may have a higher hunting risk than migration, with residents more severely restricted by available dry land and consequently more likely to come into contact with people utilising these areas. However, this may simply reflect extensive outreach activities and community contacts in breeding area villages (Sum Song, 2009), compared to non-breeding areas, where hunting was more likely to go unreported as a result. The impact of hunting on such a fragile population must not be disregarded and efforts to combat it, with particular focus in the wet season in both breeding and non-breeding areas, need to be strengthened.

Whilst floricans were tagged at a range of dry sites supporting the core population of the species remaining in Cambodia, small subpopulations have been located in grassland sites to the north and west of the Tonle Sap lake (Gray et al., 2009). The status of floricans in these

other areas should be reassessed (the first and only assessment was in 2005) and, if they persist, consideration should be given to migratory patterns and wet season areas utilised by these birds. It is not known whether the remnant breeding populations located outside of the floodplain also migrate (Gray et al., 2009), as they are less likely to be forced to move by extensive flooding. Additional telemetry of individuals breeding in sites from further north and to the west of the lake is desirable to clarify patterns for the whole Cambodian population.

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Chapter 4:

Non-breeding habitat use of Bengal floricans in Cambodia

and implications for conservation

Abstract

In Cambodia, habitat use of the Critically Endangered Bengal florican has been established for the breeding season, when they occupy grasslands in the floodplain of the Tonle Sap lake. However, when these areas flood during the wet season, the location and habitat requirements of floricans were previously little known. This chapter uses wet season locations of satellite-tagged floricans to assess habitat use relative to availability. This was addressed first in terms of broad habitat classes, relating telemetry locations to a supervised habitat classification of a satellite image, and second by comparing field-based measures of habitat covers between used and random locations. Floricans were found to select areas of open savanna and medium-canopy forest and to avoid agriculture and closed-canopy forest. Analysis of field data showed increasing probability of florican occurrence with increasing grassland cover, and decreasing probability of occurrence with increasing plantation cover. Threats faced by birds from the disjunct northern and southern breeding areas were different, with the spread of plantations a major concern in the north, and extensive agriculture, with very little remaining suitable habitat, in the south. Currently the floricans' prospects are uncertain: in the north protected areas are not widely used owing to lack of suitable habitat contained within them, and many florican locations instead fall within areas of planned plantation developments, whilst in the south there is no habitat provision or protection. Different approaches are therefore required for the two regions, with protection of small reserves containing high use areas recommended in the north, whilst more drastic measures such as habitat creation/restoration are urgently required in the south.

Introduction

The previous chapter examined the timing and pattern of migratory movements between breeding (dry season) areas in the Tonle Sap floodplain and non-breeding (wet season) sites, and quantified home range size and site fidelity for Bengal floricans during the wet season. In addition to identifying the localities that are used it is also important to understand which habitats and landuses are selected and utilised by floricans during the wet season. Previous research has established dry season habitat preferences of floricans (Gray et al., 2007, 2009), but when these sites flood in the wet season and floricans migrate away from the breeding grasslands, habitat preferences are not known. Owing to rapid landuse change in Cambodia in recent years it was considered vital not only to protect breeding grounds but also include protection of non-breeding habitats, and in 2008 two Bengal Florican Conservation Areas (BFCAs) were established in those parts of the region where floricans had been recorded or were thought to occur, but whether these adequately overlapped the species's habitat requirements was unknown. Now that we have a better understanding of the distribution of floricans in the wet season, it is possible also to examine their habitat requirements, which is a key remaining aspect that needs to be addressed to ensure that conservation initiatives for the species provide suitable conditions for its survival in both the breeding and non-breeding areas.

This chapter aims to determine habitat preferences of migratory floricans during the wet season (1) by relating florican satellite telemetry locations (from the 2008, 2009 and 2010 wet seasons) to a map of broad habitat types produced by supervised classification of a satellite image, and (2) from field data collected at florican satellite locations and random points at the end of the 2009 wet season (for locations obtained in 2008 and 2009). In addition, changes over the last decade in broad habitat cover in the wet season areas are quantified and florican location fixes examined in relation to landuse and potential threats. The suitability of protected Bengal Florican Conservation Areas (BFCAs) in the light of florican habitat requirements is then considered.

Methods

Satellite tracking

Bengal floricans were fitted with satellite transmitters as described in Chapter 3. A total of 648 wet season location fixes (from approximately August–December) were obtained from the 14 migratory floricans (eight from northern and six from southern sites) over the three years 2008–2010 and used to determine habitat preferences. Habitat was assessed in 2009 (for both remotely sensed and field data). Only GPS (error radius of up to 100m) and Argos location classes 3 (error radius up to 250m) and 2 (250–500m error radius) were used, contributing 17%, 35% and 48% of location fixes respectively. In addition, home range kernels were produced for eight individuals (four from northern and four from southern sites) that had at least 24 locations (GPS, LC3 or LC2) in a season, as described in Chapter 3.

Habitat mapping

An up-to-date habitat cover map was produced by supervised habitat classification (maximum likelihood) of a Landsat 7 ETM+ satellite image (Path 126/Row 51, bands 3, 4, 5 and 7) from February 2009. Habitat data were collected from 50m radius ground-truth points, visited at the end of the 2009 wet season (January 2010). Plots of 50m radius were appropriate (based on the recommendations in Justice and Townshend, 1981), given pixel dimensions (30x30m) and the error in the georeferenced image (of approximately 0.5 pixels) to which ground-truth points would be related. Ground-truth points were selected from across florican breeding and non-breeding areas. Points were chosen randomly, stratified by known habitat types and also using unsupervised habitat classification categories, to ensure that the full range of spectral responses was sampled. Ground-truth points were assigned to habitat categories, which were then combined into fewer, broader categories during analysis until they could reliably be separated by the satellite habitat classification (final categories used are shown in Table 1). Classification was conducted in ArcGIS (see Chapter 2 for methods) using 1,119 training ground-truth points, collected from across the range, whilst an additional 158 independent validation points were selected from the study areas. The overall accuracy of the classification was 69% with a KHAT statistic of 0.57. The accuracy of individual habitat classes is shown in Table 2. Agriculture and wetland were reliably distinguished from other habitats and accuracy

for the three classes of forest cover was good, but occasional misclassifications occurred among forest cover classes.

Table 1. Habitat classes assigned to ground-truth points and used in classification of the satellite image.

Habitat class	Definition
Closed-canopy forest/scrub cover	> 40% tree canopy cover (natural forest and plantation) or > 50% scrub cover, remaining area grass cover
Medium-canopy forest/scrub cover	15–40% canopy cover or 26–50% scrub cover, remaining area grass cover
Open savanna/grassland	<15% canopy cover or <25% scrub cover, remaining area grass cover
Agriculture	Mostly consisting of rice, but other crops included sesame, cassava, watermelon and peanut
Wetland	Open water or wetland areas present at the end of the wet season (considered permanent features; much of the land is subject to temporary shallow flooding during the wet season)

Table 2. Error matrix for supervised satellite habitat classification using 158 independent validation points. Correct classifications are shown in bold.

	Classification habitat						
Ground-truth habitat	Closed	Medium	Open	Agriculture	Wetland	Total	Accuracy
Closed-canopy forest	**15**	6	0	3	0	24	63%
Medium-canopy forest	3	**13**	5	0	0	21	62%
Open savanna	8	13	**29**	0	0	50	58%
Agriculture	6	2	6	**36**	0	50	72%
Wetland	0	0	0	1	**12**	13	92%
Total	32	34	40	40	12	158	69%

Analysis of habitat selection by Bengal floricans

<u>From remotely sensed data</u>

First, used habitat was determined for each individual for which home range kernels were produced. Home range kernels (95% and 50%) were overlain on the satellite habitat classification map and the percentage habitat composition within these calculated. Second, all wet season location fixes (pooled across years for individuals with multiple migratory seasons) were buffered according to their maximum error radius (i.e. GPS: 100m, Argos location class 3: 250m, location class 2: 500m) and the habitat composition of the buffered fixes extracted from the satellite habitat classification map and averaged for each individual. Buffering locations helps account for location error and ensures the habitat type actually used is included, although it can produce conservative selection estimates as unused habitat is also incorporated (Rettie and McLoughlin, 1999; McLoughlin et al., 2002).

Habitat availability was determined separately for northern and southern birds, as their wet season areas were disjunct (with closest locations being separated by 50 km). For each population, the landscape available to floricans to sample and settle was defined as that delimited by the aggregate area currently used by all birds, a common approach (Thomas and Taylor, 1990) which avoids arbitrary delineation of availability (Aebischer et al., 1993). A Minimum Convex Polygon (MCP) was produced from all location fixes of all birds for each area. To ensure that the 95% kernel home ranges were contained within the availability areas, both MCPs were then buffered by the mean radius of the 95% kernels (4.18 km), to produce the final availability areas for the north and south. The year 2010 produced a particularly dry wet season (see Chapter 3) and unusually low water levels made part of the floodplain available, and as a result in that year two of the southern migratory birds utilised areas on the edge of the floodplain (which would usually be under water during this season). Therefore habitat availability in the south was determined separately for 2010. In the north there was no use of the floodplain by migratory individuals in 2010.

For each habitat class, use relative to availability was presented as the mean (± SE) of the natural log of the ratio of percentage use to percentage available extent (termed the 'log-ratio') determined for each individual. The degree to which use differed from that expected by chance, given availability, was assessed by compositional analysis (Aebischer et al., 1993),

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using each individual as the experimental unit. Compositional analysis is an extension of multivariate analysis of variance, and for each pair of habitats in turn it examines the log-ratio of relative use (e.g. of habitat 1 to habitat 2) to relative availability (of habitat 1 to habitat 2). The significance of Wilks's lambda and of t-values was determined by randomisation tests (with 1,000 iterations), overcoming the requirement for log-ratio differences to have multivariate normal distribution (Aebischer et al., 1993). Wetland was excluded from the analysis as a minor component of the landscape and only occurring in the home ranges of two individuals (comprising <2% of their home range habitat). For habitats not used by an individual, the 0% value was replaced by 0.01% (an order of magnitude smaller than any actual use percentages) to allow log-ratios to be calculated (as recommended by Aebischer et al., 1993). For home range kernel habitat use, a single analysis was conducted with all eight individuals, but habitat availability was specified separately for northern birds (all years), southern birds in 2008–09 and southern birds in 2010. For use determined by buffered location fixes, there were sufficient individuals to run separate analyses for the northern and southern birds (with availability determined as for home ranges). Compositional analyses were conducted using Compos Analysis (Smith, 2005), an Excel macro.

From field data

A total of 97 wet season migratory location fixes obtained in 2008 and 2009 from six individuals were visited at the end of the 2009 wet season (in January 2010). Percent cover of vegetation types (listed in Table 3) were estimated within a 100m radius plot centred on each location fix. Plots of 100m radius were considered appropriate for assessing habitat selection for this species and also took into account location error (Hingrat et al., 2006). In order to sample habitat potentially available to each individual, 4 km buffers were generated around all locations of that individual and dissolved to provide a polygon encompassing landscape within its perception range. This was considered preferable to relating habitat at fix locations to that within the home range kernel, owing to small sample sizes making kernel estimation unreliable for some individuals. Random points (to represent habitat availability) were generated within these buffers in ArcGIS and sampled as for location fixes (used habitat). Data on used and available habitat were pooled from all individuals; although this creates pseudoreplication and unequal contribution of habitat use from individuals, it is common practice (Thomas and Taylor, 1990) and considered appropriate when the sample size of individuals is small (Millspaugh and Marzluff, 2001). This precludes use of the preferable method of averaging coefficients from logistic regression models created for each individual, which treats the

individual as a random effect (Millspaugh and Marzluff, 2001). Points consisting of bare ground resulting from recent ploughing, along with points recently planted with young plantation saplings, were excluded, as their vegetation cover at the time of use (up to four months prior to sampling) could not be determined. Wetland cover was again excluded from analysis. Vegetation types that did not differ in percent cover for used and available plots (compared by univariate Mann-Whitney U tests: $p < 0.1$) were excluded from subsequent multivariate analysis by a logistic regression model. None of the remaining variables was strongly inter-correlated ($r > 0.7$) and all were therefore retained as independent predictors. Residuals were examined to check for any points (a) exerting an excessive influence on the model (high leverage) or (b) for which the model fitted poorly. Neither was found. The logistic regression model was developed in SPSS version 16, by backward elimination with variable retention judged by the change in log-likelihood (-2LLR, tested by chi-square).

Table 3. Vegetation cover types in 100m radius plots along with variable codes and definitions.

Vegetation cover types	Variable code	Definition
Grassland	GRL	Grass cover
Fallow field	FLF	Grass cover (usually short and heavily grazed), evidence of field boundaries
Crop	CRP	Mostly rice, but also some vegetable crops
Shrub	SHR	Natural woody vegetation < 4m in height
Tree canopy	TRC	Natural woody vegetation > 4m in height
Plantation	PLN	Cover of acacia, rubber or eucalyptus plantation canopy
Bare ground	BGR	Exposed soil, no vegetation cover

Habitat change 2000–2009

Change in habitat composition of the northern and southern study areas was assessed by comparing the habitat classification map for 2009 with a landcover map for 2000 (as used in Chapter 2, JICA and Ministry of Public Works and Transportation, Cambodia, 2000), which had a reported accuracy of around 80% (JICA and Ministry of Public Works and Transportation, Cambodia, 2003). As the percentage canopy cover and scrub density were mostly unspecified in the 2000 landcover map, specific JICA landcover classes are presented (with the exception of agricultural and wetland classes, which could be grouped and directly compared). JICA 'grassland' and 'woodland and scattered trees' (for which canopy cover is specified as <10%) were considered to be comparable to our open savanna category (tree canopy <15% or scrub <25%), whilst JICA categories of 'shrubland', 'abandoned field covered by shrub', 'dry

deciduous (open) forest' and 'plantation (rubber)' were compared with our medium and closed (which included plantation) forest categories.

Use in relation to landuse designation and threats

Florican location fixes were overlain on landuse types in the north (where landuse types are known and varied) that have implications for habitat persistence: protected BFCAs, active land concession (under development for plantation) and planned land concession (designated and future conversion highly likely). Habitat composition of the BFCAs (excluding 8.7 km^2 [8%] of Trea Sameakki BFCA that was not covered by the Landsat scene) and the northern MCP (generated from location fixes, minus the BFCA areas) were compared to assess the habitat suitability of the BFCAs.

Results

Habitat selection

Florican wet-season location fixes and home ranges (for eight individuals with >24 fixes in a season, excluding non-migratory individuals) for the 2008–2010 wet seasons are shown overlain on habitat classes in Figure 1. The northern study area consisted of similar proportions of closed forest, medium forest, open savanna and agriculture (Table 4). In contrast, the southern study area for 2008–09 was dominated by agriculture, with limited extent of closed forest and only small amounts of open savanna and medium forest. In the dry year of 2010, there was increased wet-season availability of open savanna, occurring in the floodplain.

At the scale of 95% kernel home ranges, in relation to the study landscape, Bengal floricans used open savanna and medium forest more than expected based on available extent, whilst closed forest and agriculture were used significantly less (OPN > MED >>> CLS > AGR: Figure 2a). The same rank ordering of habitats was exhibited for 50% kernel cores, but only open savanna was used more than expected (medium forest was avoided) and was used significantly more than agriculture and closed forest (OPN > MED > CLS > AGR).

At the scale of individual telemetry fixes (648 locations from 14 individuals), it was possible to conduct compositional analysis separately for northern (n=8) and southern (n=6) birds,

revealing differentiation in habitat use between these regions (Figure 2b). In the north, open savanna and medium forest were selected and used significantly more than either closed forest or agriculture, whilst agriculture was also used significantly less than closed forest (OPN > MED >>> CLS >>> AGR). In the south, all habitat classes had negative log-ratios (but with SE for open savanna extending to a positive value); none was used significantly differently from each other and variance was high. This probably reflected the greater extent of the less preferred agricultural landclass and limited availability of other cover types.

In terms of field-based measures of vegetation, grassland cover was significantly greater in used than in random plots, whilst cover of fallow, crop and plantation was significantly less (Figure 3). The minimal logistic regression model retained two significant predictors, with greater probability of florican use with greater grassland cover and decreasing with greater plantation cover (Table 5).
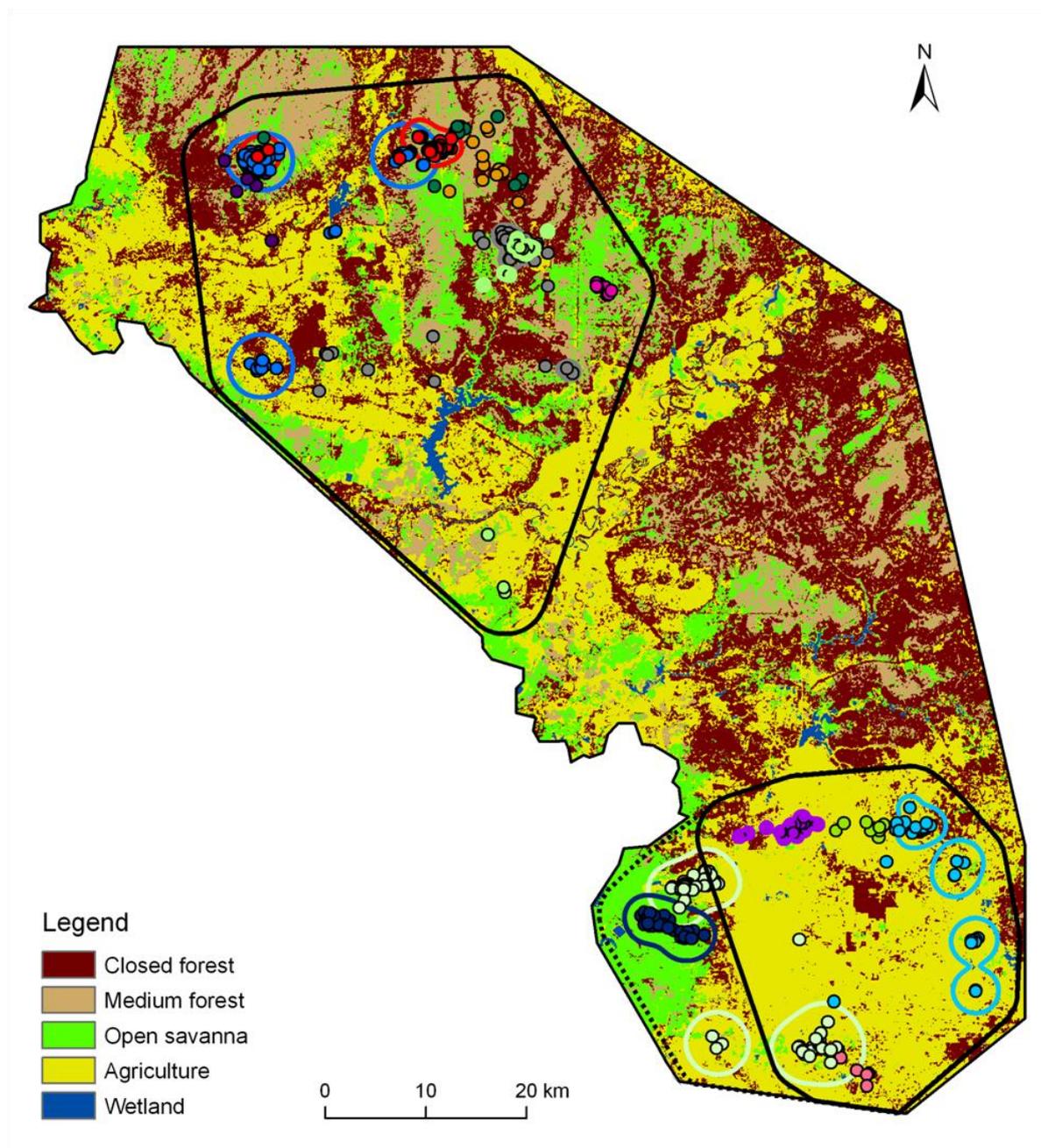
Figure 1. Supervised satellite habitat classification of florican wet season migratory areas. Wet season location fixes (2008–2010) and 95% kernel home ranges (single season, for eight individuals with >24 locations) are overlain. Individuals (fixes and home ranges) are separated by colour. Study areas (habitat availability for compositional analysis) are outlined in black for the north (2008–10) and south (2008–09), with a dashed line showing the additional area for the south in 2010.

Table 4. Habitat availability within areas used by Bengal florican during the wet season, separately for northern (all years) and southern (2008–09 and 2010) study areas.

| | Area km^2 (percent composition) | | |
| | North | South | |
Habitat	2008–10 area	2008–09 area	2010 area
Closed forest	520 (29)	107 (13)	137 (12)
Medium forest	378 (21)	3 (0.3)	9 (1)
Open savanna	304 (17)	13 (2)	132 (12)
Agriculture	567 (32)	714 (85)	820 (74)
Wetland	26 (1)	5 (1)	7 (1)
Total area	1795	842	1105
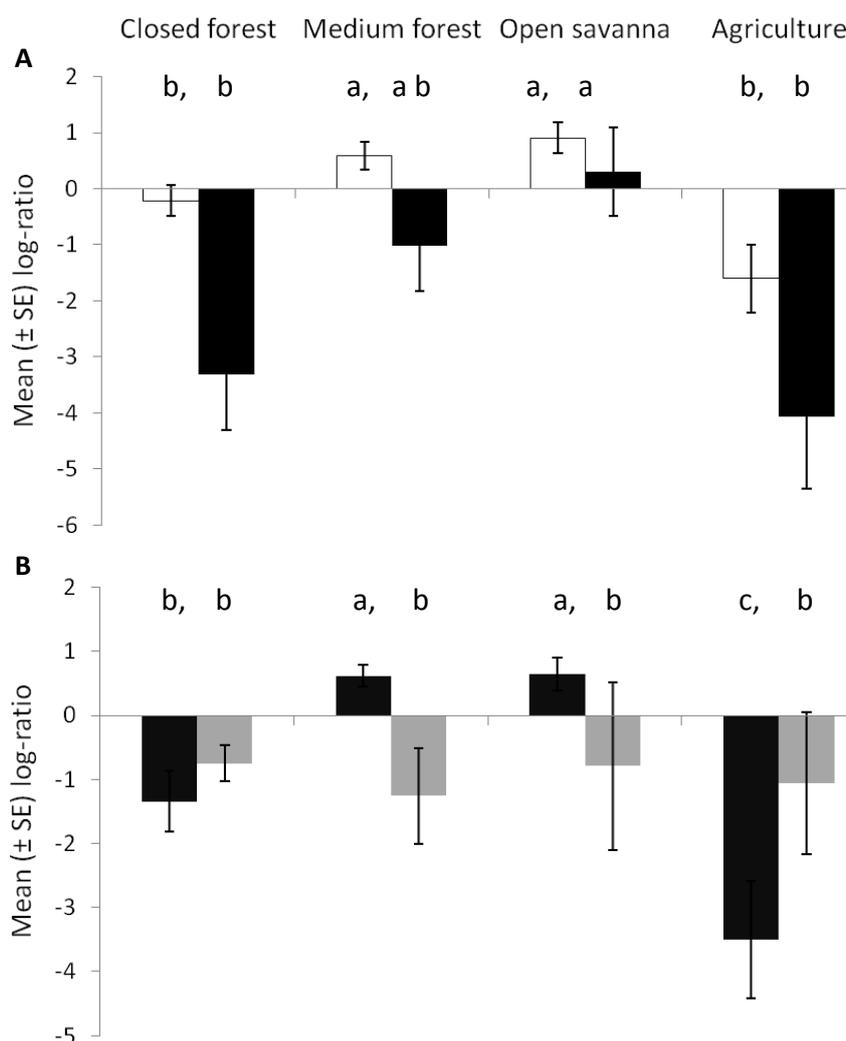
Figure 2. Mean (± SE) log-ratios of used/available habitat for (A) 95% (hollow bars) and 50% (filled bars) kernel home ranges for eight floricans (pooled across both the northern and southern study areas), and (B) buffered telemetry fixes for 14 floricans, eight from northern (black bars) and six from southern (grey bars) areas. Letters indicate significant differences between habitats, with (A) for 95% followed by 50% kernels, and (B) for northern followed by southern fixes, based on compositional analysis: habitats sharing a superscript do not differ significantly in the extent of their use, controlling for availability.
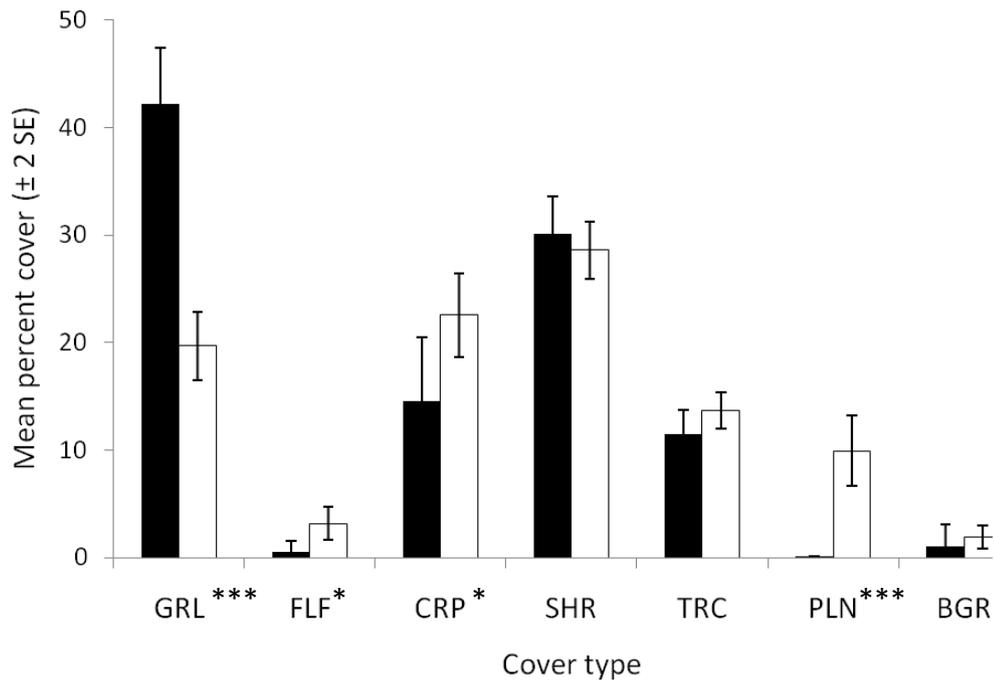
Figure 3. Comparisons of percentage cover of vegetation types for used plots (solid bars) and random plots (hollow bars). *p<0.05, ***p<0.001 (Mann-Whitney U tests). SHR and TRC were excluded from subsequent analysis in the logistic regression model (p > 0.1), whilst BGR was included (p < 0.1).

Table 5. Minimal logistic regression model comparing field measures of vegetation between used and random points.

Variables retained	B (SE)	Wald	Exp(B) (odds-ratio)	95% CI for Exp(B) Lower	Upper
GRL	0.029 (0.005)	39.019***	1.029	1.020	1.039
PLN	-0.723 (0.345)	4.279*	0.485	0.247	0.955

Nagelkerke r^2 = 0.246, 75% correctly classified, x^2 = 69.8, p < 0.001.
*p<0.05, ***p<0.001

Habitat change 2000–2009

Habitat composition of the northern and southern study areas changed between 2000 and 2009 (Table 6). In the north, the percentage cover of the denser vegetation classes (medium and closed forest) doubled between 2000 and 2009, whilst agricultural cover was approximately halved. Open savanna cover remained little changed. The reverse pattern was

seen in the south, with a decrease in medium and closed forest covers and an increase in agricultural cover, particularly great for the area typically (2008–09) available once the floodplain was inundated. As in the north, cover of open savanna remained fairly constant.

Landuse

Florican location fixes in relation to land designations are presented in Figure 4. Only a small area of Trea Sameakki BFCA was used by tagged birds, with no locations occurring in Tuol Kruel Phan Nheum (both BFCAs extend beyond the northern study area). The habitat within the BFCAs is dominated by forest cover compared to the northern study area as a whole, which incorporates more agricultural land (Table 7). Two-thirds of Trea Sameakki is medium forest, whilst over a third of Tuol Kruel Phan Nheum is closed forest, with only 6% open savanna. Four of the eight northern birds used the active land concession being developed for plantation, and three of those four, along with one additional bird, used the planned land concession areas.

Table 6. Change in percent habitat composition of the northern and southern study areas between 2000 and 2009. The southern area is examined separately in terms of available extent in 2008–09 and also in the drier season of 2010.

2000: JICA classes	2009: Satellite classification classes	Northern		Southern (available 2008–09)		Southern (available 2010)	
		2000	2009	2000	2009	2000	2009
Agriculture	Agriculture	**58.7**	**31.6**	**68.9**	**84.8**	**64.5**	**74.2**
Grassland		9.4		1.1		12.7	
Woodland scattered trees (<c10%)		5.4		0.0		0.0	
Total	Open savanna	**14.8**	**16.9**	**1.1**	**1.5**	**12.7**	**11.9**
Shrubland	Medium forest	3.6	21.1	0.3	0.4	0.2	0.8
Abandoned field covered by shrub	Closed forest (inc. plantation)	18.1	28.9	15.3	12.7	11.7	12.4
Dry deciduous (open) forest		3.4		0.0		0.0	
Plantation (rubber)		0.0		14.0		10.6	
Total	Total	**25.1**	**50.0**	**29.6**	**13.1**	**22.5**	**13.2**
Wetland	Wetland	**1.4**	**1.4**	**0.4**	**0.6**	**0.3**	**0.6**

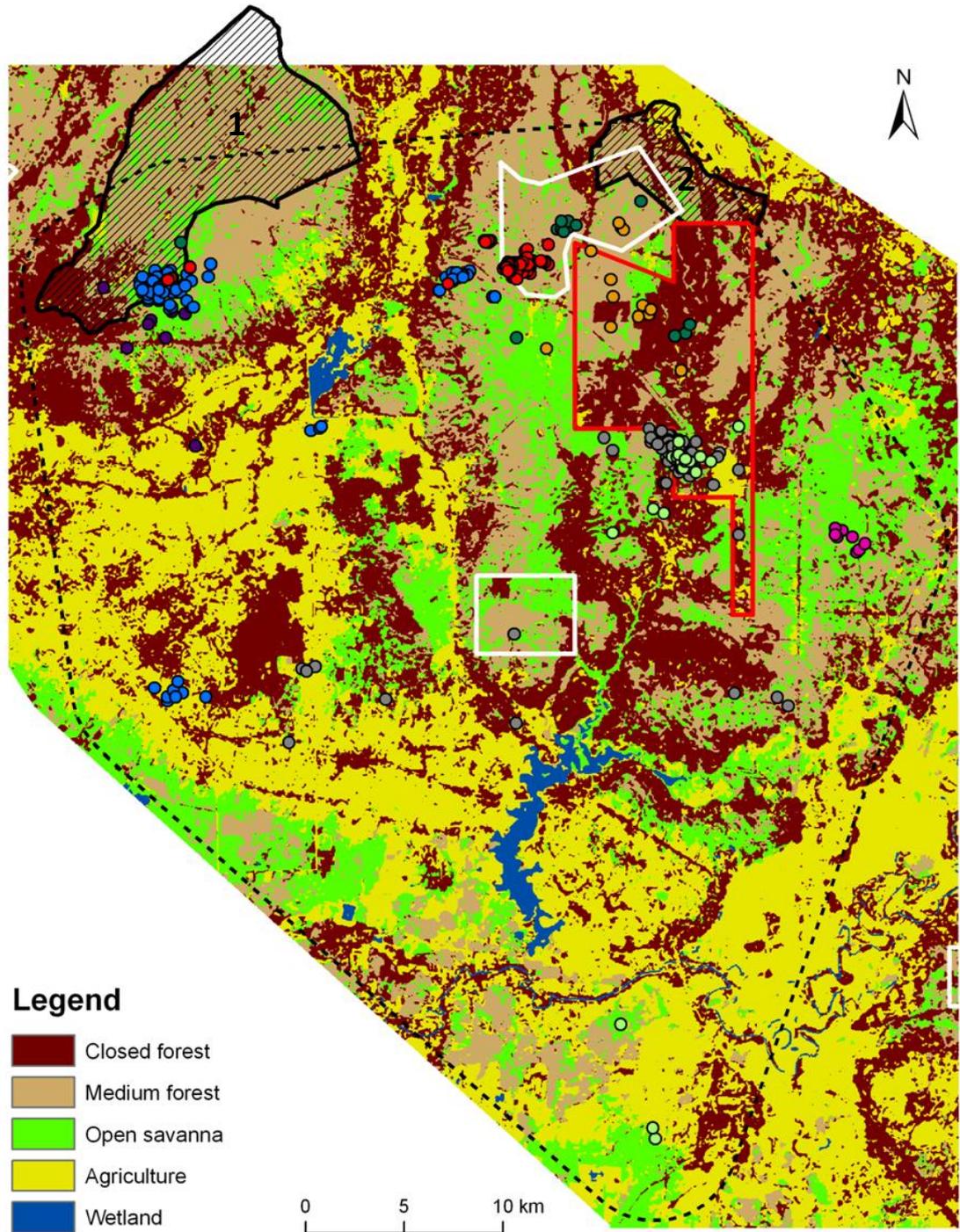**Figure 4.** Landuse in the northern study area, showing BFCAs (black outline with hatched fill): 1, Trea Sameakki and 2, Tuol Kruel Phan Nheum, along with an active land concession (red outline) and planned land concessions (white outline) and overlain with location fixes (individuals separated by colour) on the habitat classification. The northern study area is shown by a dashed black outline.

Table 7. Percentage habitat composition compared between Trea Sameakki and Tuol Kruel Phan Nheum BFCAs and the remainder of the northern study area.

Habitat	Northern study area (excl. BFCAs)	Bengal Florican Conservation Areas	
		Trea Sameakki	**Tuol Kruel Phan Nheum**
Closed forest	29.1 %	16.4 %	38.4 %
Medium forest	19.4 %	66.3 %	45.7 %
Combined closed & medium forest:	**48.5 %**	**82.7 %**	**84.1 %**
Open savanna	17.1 %	15.8 %	5.5 %
Agriculture	32.9 %	1.5 %	10.4 %
Wetland	1.5 %	0.0 %	0.0 %

Discussion

Non-breeding areas available to floricans consist of dry dipterocarp forest, ranging from open savanna (mostly grass cover with scattered trees and considerable evidence of harvesting) to medium and closed forest, along with agriculture (mostly rice but also vegetable crops) and plantation (acacia, rubber and eucalyptus).

Assessing habitat preferences using home range kernels of floricans from both northern and southern areas gave a general understanding of habitat use, with extent of open savanna and medium canopy forest within 95% kernels selected above that expected from availability across the study areas. Assessing 50% kernel habitat use is likely to give a more accurate indication of important habitats, as less of the unused (peripheral) habitat is likely to be incorporated and analysis can focus on the core area of the home range. The only habitat cover selected in 50% kernels was open savanna, with mean log-ratios for medium forest having a negative value suggesting avoidance at this scale (although not significantly different from open savanna). Closed forest and agriculture were consistently avoided, and much more strongly at the 50% kernel level.

Wet season habitat availability differed considerably between northern and southern areas. In the north, floricans had access to similar proportions of the different habitat types, whilst in the south the landscape was dominated by agriculture, with some closed forest but scarcely any open savanna or medium forest. In the light wet season of 2010, the amount of savanna available to the migratory floricans in the south was increased, as a section of the outer floodplain (unusually) remained flood-free, although whether migratory individuals regarded

this as available may have been constrained by site fidelity. Conducting habitat analyses separately for northern and southern birds, based on buffered location fixes, showed a pattern in the north similar to the 95% home range kernel habitat use, with open savanna and medium forest selected, closed forest significantly less preferred and largely avoided, and agriculture strongly avoided (and significantly more so than closed forest).

In the south, however, the pattern of habitat use was unclear, with considerable variation among individuals and no significant differences in use among habitat types (and only the standard error of the mean log-ratio for open savanna extended to a positive value). This is likely to be due to the majority (85%) of the southern area being agriculture (74% for the 2010 study area), with very little open savanna or medium forest available, clearly the preferred habitats when sufficiently abundant. The high variability among individuals may well reflect a lack of suitable habitat, with different individuals adopting different strategies to cope with this. For 95% and 50% kernels (northern and southern birds pooled), as well as for northern birds (based on buffered location fixes) exposed to all habitat types, agriculture was consistently the most strongly avoided habitat type (and was also found to be avoided by floricans in the breeding season; Gray et al., 2009), yet in the south there were few other habitat options. This problem is likely to have grown larger recently, as agricultural cover has increased from 69% to 85% in the nine years since 2000 (for the area available under normal wet season conditions).

When habitat use was examined in terms of field-based structural measures, rather than by satellite classification of broad landcover types, probability of florican use increased as grassland cover within the 100 m radius increased. Conversely, as plantation cover increased, probability of use declined. Whilst univariate comparisons showed fallow field and crop covers also to be significantly lower in used than available plots, plantations were even more strongly avoided than agricultural covers. The strong avoidance of plantations, while entirely expected, is particularly worrying given that almost half of all fixes from individuals tagged in the north fell within either active or planned concessions in which plantations will be developed. In 2000, there was no plantation cover shown on the JICA landuse map and whilst plantation could not be distinguished from the closed forest category in analysis of satellite imagery from 2009, it seems highly likely that the increase in the denser forest covers reflects the spread of plantations (C. Packman pers. obs.).

Florican habitat use in the breeding and non-breeding seasons differs considerably. In the breeding season, open grassland areas are occupied, and tall vegetation covers avoided (Gray et al., 2007), whilst we found use not only use of open savanna but also of medium density forest areas in the non-breeding season. Bustards are generally considered to be birds of open habitat, but show varying degrees of use of more closed habitat types (Collar, 1996). Open habitats may be of greater importance for bustards during the breeding season, offering good visibility for male displays (Jiguet and Bretagnolle, 2001; Gray et al., 2007) and a plentiful supply of insects for females with chicks. Vegetation height is likely to be a trade-off between concealment from predators and visibility for display purposes, as reported in other bustard studies (Martínez, 1994; Salamolard and Moreau, 1999; Silva, 2004). In the non-breeding season, high visibility is not required for displays and concealment from predators is likely to take priority (as hypothesised for little bustards *Tetrax tetrax*, Silva, 2004), although dense vegetation (avoided by floricans) could hamper movement and also conceal predators.

As floricans from northern and southern areas do not overlap in their use of non-breeding landscapes, conservation measures must meet the requirements of the two populations independently. The findings presented here suggest that different threats and challenges exist in the north and south. Currently, the availability of suitable habitat is much better for the birds in the north, as suggested in Chapter 3 owing to their smaller home range sizes, while little other than agriculture is available to birds in the south, where home ranges were larger. The pattern of larger home ranges in areas of poorer habitat has been observed in other species, such as the capercaillie *Tetrao urogallus* (Gjerde and Wegge, 1989). However, despite the greater availability of suitable habitat in the north, the threat to habitat there is very high and urgently needs to be addressed. The birds' high use of land concessions is unfortunately in rather stark contrast to their low use of protected areas, with only a small section of Trea Sameakki BFCA (where open habitat is concentrated) being used and no locations from tagged birds received from Tuol Kruel BFCA (which has greater cover of closed forest). Field surveys conducted by the Wildlife Conservation Society have located florican in a wider area of Trea Sameakki, but none as yet in Tuol Kruel (van Zalinge et al., 2009, 2010). This may be because areas of 'good' forest were prioritised for protection, when floricans are actually using degraded areas of forest that are kept open by wood harvesting. The areas originally proposed for the BFCAs incorporated much more of the suitable open savanna habitat and then-available florican records (and more of the areas that subsequently contained florican fixes), but were rejected because concessions had been granted in these areas (perhaps because favoured by plantation owners as there are fewer trees to clear prior to planting, and possibly

also because seen by the authorities as less pristine habitat and therefore more acceptable for conversion). BFCAs were arguably established in the best places possible given the available distribution data and political options at the time, but the new data presented in this chapter confirm the need to review their boundaries and propose improvements (T. D. Evans pers. comm.). Methods to improve habitat suitability within the current BFCAs (such as management to create more open forest/grassland) should be considered. Given the extent of land concessions and the difficulty of establishing any additional large protected areas that would encompass the dispersed sites in use, the only option may be to focus on creating a number of small reserves in the patches of suitable habitat where floricans have been located. This will demand more comprehensive data on occupied sites than are currently available, although an initial, incomplete list of candidate sites can be drawn up from fixes in this study and other field observations. All florican locations in open savanna and medium forest displayed evidence of wood cutting (helping to keep the habitat open), and therefore this should be allowed to continue in any reserves, but human disturbance and the potential for hunting should be kept in mind (see Chapter 3) and discussed with local communities regarding reserve use.

In the south, more drastic conservation measures may be required to restore or create suitable habitat, as little remains, with most having being converted to agriculture. In both regions, the strong site fidelity of floricans in the wet season (see Chapter 3) needs to be considered, as any creation of new suitable habitat or protection of areas that appear suitable based on habitat may fail to attract floricans faithful to specific areas, even when no suitable habitat remains in them ("ghosts of habitats past" Knick and Rotenberry, 2000). Lane et al. (2001) found great bustards *Otis tarda* to be poor colonisers of new areas of suitable habitat, preferring to remain in traditional sites of occupancy, with conspecific attraction thought to play a more important role. Whilst the degree of conspecific attraction of floricans in wet season areas is not known, a quarter of those sighted during surveys (conducted by the Wildlife Conservation Society since 2005) were observed with at least one other florican (mostly in twos: Son Virak and R. van Zalinge pers. comm.). Therefore selecting potential areas for protection (in the north) may start with identifying areas of suitable habitat, but presence of floricans must also be confirmed, and similarly for restoration or creation of new habitat (in the south) known florican locations must form the basis of area choice. Given site fidelity, consideration could be given to habitat restoration in areas shown by JICA to have supported grassland or open canopy forest covers in the recent past.

Understanding of wet season habitat requirements could be further improved by increasing the sample size of tagged birds, both in this area and in additional areas around the Tonle Sap lake, to gain a more complete picture of habitat use. Furthermore, increasing the number of location fixes received for each individual would strengthen analysis. This was a limitation in this study, as transmitters were often unreliable and locations received sporadically. Experimenting with different transmitter types and duty cycles has meant that transmitters have performed better in each year of deployment in this study (see Chapter 6). The frequency of attempted location fixes is also limited by power, which is reduced in the wet season for solar units and which needs to be regulated to ensure battery units last a complete migration cycle. In addition, in order to gain understanding of finer-scale habitat preferences, higher accuracy fixes are required so that florican locations can be determined with precision and related to specific habitat features. This would require either successful use of GPS transmitters (solar GPS units have so far not performed well here for floricans) or the use of combination radio-satellite tags (with radio-telemetry allowing greater precision but posing a considerable challenge during the wet season, as described in Chapter 3). Examination of the importance of habitat mosaics and patch size warrants investigation, along with the influence of physical factors on florican distribution such as elevation and flooding extent. Investigation into food availability in different habitats would be also be useful in examining florican distribution.

This key population of Bengal florican is clearly facing major threats not only to breeding season habitat (see Chapter 2), but also to non-breeding season habitat. To date, conservation measures have been more focused on breeding areas (where locations and habitat requirements were better known), but a lack of knowledge of non-breeding areas and habitat use has inhibited the identification and tackling of threats. Failure to address these could result in conservation efforts in the breeding areas being in vain. Conservation of migratory species is complex, with different threats often faced during different parts of the year and in different areas (Martin et al., 2007). Therefore a multi-faceted approach is required if conservation measures for species such as the Bengal florican are to succeed.

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Chapter 5:

Spatial and temporal patterns of home range occupancy and

habitat use of breeding Bengal floricans in Cambodia

Abstract

Home ranges of Bengal floricans were examined during dry season occupation of floodplain grasslands surrounding the Tonle Sap lake, Cambodia. With the use of satellite telemetry, home ranges during the core breeding period were found to be significantly smaller than those also encompassing pre- and post-breeding locations. Breeding season space use differed for males and females, with females having larger core (50% kernel) areas and a greater tendency towards multimodal home ranges. However, females remained within the exploded lek throughout the breeding season, suggesting that a 'hotspot' rather than 'hotshot' model may determine lek behaviour. There was considerable overlap in 95% kernels between tagged birds, but core area overlap only occurred between sexes. Both sexes exhibited strong inter-annual fidelity to breeding sites, even following habitat conversion, raising concerns that response to relative suitability of sites may be impeded. Grassland was the only habitat type selected, of those occurring in the floodplain, with avoidance of agricultural landuses, scrub and wetland. Smaller home ranges were found to contain a higher percentage of grassland and are therefore likely to reflect better habitat quality. Records of nesting activity show that the nesting period extends beyond the period of male display activity, and appeared to peak with late dry season rains. Conserving extensive areas of the male exploded lek is likely also to meet the needs of breeding females. However, home ranges of both sexes are an order of magnitude larger than previously found, with implications for the amount of land required to support the population. In addition, the greater mobility of males found suggests current census methods may potentially over-estimate population numbers.

Introduction

Understanding breeding season landscape use is of considerable importance for threatened species, as access to suitable habitat during this critical period may determine the ability of a population to recover. For polygynous species exhibiting sexual dimorphism, males and females can differ substantially in their space requirements and habitat use during the breeding season. Clearly it is important for conservation measures to consider the needs of both sexes (Ruckstuhl and Neuhaus, 2006) to ensure productivity is maximised and the requirements of the whole population are met.

The Critically Endangered Bengal florican *Houbaropsis bengalensis* is a polygynous bustard. Like the majority of bustards, floricans are a lekking species (Collar, 1996), with males forming 'exploded' leks (Gilliard, 1969): each male defends its own territory both for display and for feeding (hence larger than a typical lek territory, which is used for display only), but territories are clustered together within the landscape. Females visit leks to mate but males have no involvement in raising chicks. The extent to which female floricans may use these dispersed leks for foraging and nesting, in addition to obtaining matings, is unclear (Gray et al., 2009). Thus, whether this lek system represents a 'hotshot' system, whereby female choice is based solely on male quality, or 'hotspots', whereby males monopolise areas containing resources important to females (Beehler and Foster, 1988), as found for example in Houbara bustard *Chlamydotis undulata* (Hingrat et al., 2008), is unknown. Bengal floricans exhibit sexual size dimorphism, although this is reversed relative to all other bustards exhibiting size dimorphism with the exception of Lesser floricans *Sypheotides indica*, as females are considerably larger than males (Collar, 1996). The largest remaining population of Bengal floricans breeds in the grasslands of the Tonle Sap lake floodplain, Cambodia, during the dry season (Gray et al., 2009). In the wet season there is partial migration (dependent on the extent of flooding: see Chapter 3) to areas of open dry dipterocarp forest.

A previous radio-tracking study conducted by Gray et al. (2009) at Stoung-Chikreng, a floodplain grassland site on the border of Kompong Thom and Siem Reap provinces, established male distribution and home range extent during the core period of display activity (mid-February to early June), when males seek to attract mates and defend their territories within the exploded lek. The study revealed differential habitat use by males and females.

Both sexes selected burnt grassland and avoided rice fields, but females also selected taller vegetation in areas of unburnt grasslands. Female home range areas during the breeding period remained unclear, however, with some females thought to leave lek sites to nest elsewhere, in unknown areas. How pre- and post-breeding (corresponding to early and late dry season respectively) area requirements compare to that of the core breeding period for both sexes is also unknown, as the previous radio-telemetry study was restricted to the period of peak display activity. I hypothesised that both sexes are likely to be more restricted in their movements during the core breeding period, as males display in their territories and females nest. It is not known if birds occupy different areas of the floodplain prior to or following breeding. Clearly this is important to understand to ensure appropriate areas are protected.

Bengal floricans breeding in the Tonle Sap floodplain are severely threatened by very rapid conversion of grasslands to intensive commercial dry season rice cultivation (see Chapter 2). This practice involves the construction of large dams with headponds designed to hold water for irrigating rice during the dry season. In response to this threat, three Bengal Florican Conservation Areas (BFCAs) now protect 173 km^2 of the floodplain grasslands for threatened bird species and safeguard the traditional livelihoods of local communities. One potential limitation is that these areas have been selected based almost entirely on the distribution of male florican display sites, with little understanding of whether this also encompasses areas important for female reproduction. Potential differences between the sexes in breeding season spatial requirements, the exclusivity or extent of overlap among individual territories, and frequency and extent of movements both within and between breeding seasons have important implications for the amount of land required to support a florican population and the implementation and management of protected areas that aim to conserve this Critically Endangered species. Understanding the degree of inter-annual breeding site fidelity is necessary to consider the ability of the species to adapt to a changing landscape.

Here I used satellite telemetry to examine movements at temporal and spatial scales that could not previously be established by traditional radio-tracking methods. I tracked male and female floricans sampled across a range of sites distributed through the key remaining florican population in the southeast of the floodplain to determine: (1) male and female pre-breeding, breeding and post-breeding movements and home range extent in relation to the size and location of protected areas and potential differences in requirements between the sexes, (2)

the timing of recorded nesting attempts in relation to movement patterns, male display period and rainfall, (3) the extent to which males and females overlap in their home range use and whether females leave the exploded leks, (4) inter-annual breeding site fidelity of males and females (with individuals tracked for up to four consecutive breeding seasons) and (5) selection/avoidance of broad habitat types within breeding season home ranges.

Methods

Study area

Bengal floricans were tagged at five sample sites from across the core population in the south-eastern section of the Tonle Sap floodplain (in Kompong Thom and Siem Reap Provinces); see Figure 1.
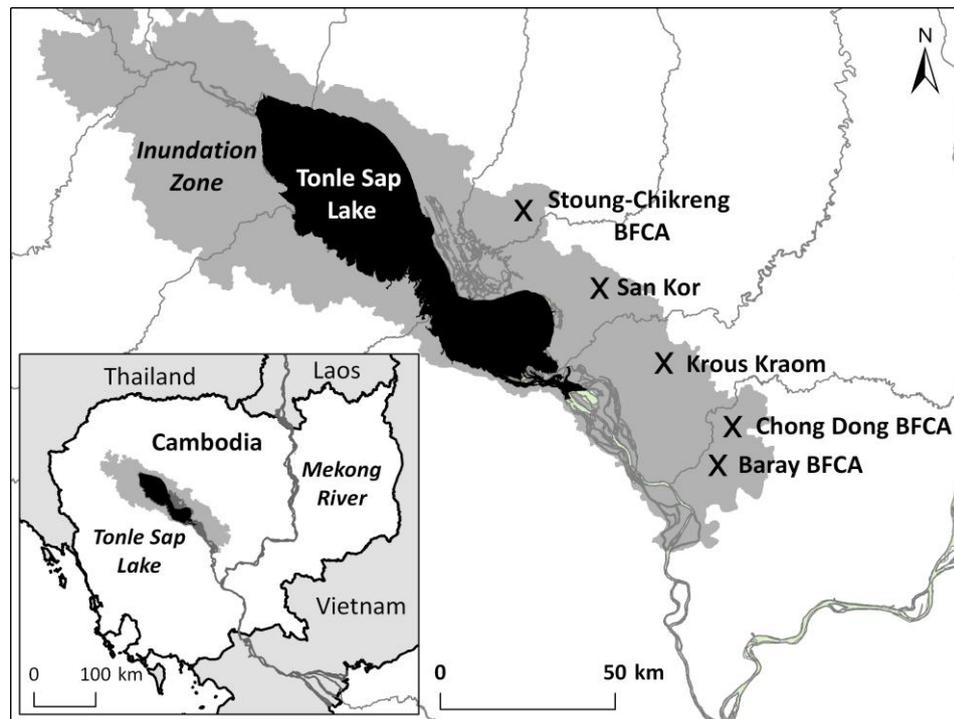

Figure 1. Location of dry season sites (X) in the Tonle Sap floodplain, Cambodia, where satellite transmitters were deployed on floricans. Black and grey shading show dry and wet season extent of the Tonle Sap Lake respectively.

Timing of breeding

Nests (containing eggs, the precocial chicks are thought to leave the nest within 24 hours of hatching) reported to the Wildlife Conservation Society were collated by month to give an indication of the nesting period. Incubation is thought to be approximately 25–28 days (Collar, 1996); potential timing of nest initiation was estimated accordingly. Nest reports were related to monthly rainfall (provided by the Kompong Thom Water Resource & Meteorology Department, Cambodia) during the dry season. Number of nests reported varied each year, probably in relation to differing degree of community contact and presence of monitoring staff. There was not thought to be a large bias in probability of encountering nests between months, although the number of people in the grasslands does vary during the breeding season with the timing of rice harvesting and ploughing.

It was not possible to locate the nests of satellite-tagged females as fixes had a location error of up to 500m and were irregular in frequency. In addition, nests are exceptionally well hidden and therefore only possible to locate with radio telemetry.

Satellite transmitter deployment

Satellite transmitters (Microwave Telemetry 45g solar GPS/Argos, 35g solar Argos and North Star Science and Technology 30g battery Argos) were deployed on a total of 21 Bengal floricans in February–March in the years 2008, 2009 and 2010 (Table 1). A major effort was made to deploy transmitters across a range of breeding season sites, with between two and seven individuals tagged at each of five sites.

Table 1. Deployment of satellite transmitters by site, sex (M = male, F = female) and year.

| Year | Number of transmitters deployed at sites | | | | |
	Stoung-Chikreng	San Kor	Baray	Krous Kraom	Chong Dong
2008	M:1	M:1	M:1	n/a	n/a
2009	F:2	F:2	M:2, F:1	n/a	n/a
2010	F:2	M:1, F:1	M:2, F:1	M:2	M:2
Total (M:12, F:9)	**5**	**5**	**7**	**2**	**2**

Home ranges

Home ranges were produced for each individual, separately for each dry season tracked. Dry season locations were determined as those received between arrival on the breeding grounds at the onset of the dry season (mean all years: 12 December) and departure at the onset of the wet season (mean all years: 31 August). For sedentary individuals that did not migrate, locations for inclusion were determined from the average arrival and departure dates of all migratory birds, in that year. For the most recent (2011) dry season, locations up to 26 July 2011 were used. Home ranges were also produced for the core breeding period of the dry season, from mid (14) February to early (7) June, based on male display activity (Davidson, 2004).

Only GPS (<100m error radius) and Argos locations classes 3 (<250m error) and 2 (250–500m error) (Collecte Localisation Satellites, 2011) were used to produce home ranges. Fixes less than 15 minutes apart (a period within which a florican could easily fly across its home range) were removed prior to producing home ranges, to reduce temporal autocorrelation. When examining movement patterns and site fidelity, home ranges were produced for all individuals. However, for estimates of home range size, only those individuals that had at least 24 locations in the period of interest (the whole dry season or the core breeding period) were included. Above this threshold, there was no correlation between the number of location fixes and home range size for 50% kernels (r = -0.057, p = 0.509), 95% kernels (r = -0.125, p = 0.280) or minimum convex polygon (MCP) areas (r = -0.043, p = 0.713). The mean number of locations per individual per season was 135 (*SD* 108) with a range of 22–630 (due to variation in performance of different unit types). To allow pre- and post-breeding movements to be assessed, dry season home ranges were superimposed on individual fixes, colour-coded by month, for those individuals (*n* = 6) with at least five locations for each of the early season months (spanning December–February) following return to the breeding grounds, and also for the late season months (spanning June–August) prior to departure.

Home ranges were produced using adaptive kernels with outer 95% and core 50% isopleths. An ad hoc smoothing factor was applied, whereby the smallest proportion (using 0.05 steps) of the reference bandwidth that maintained an intact 95% contour was selected (Rodgers and Kie, 2011). If an intact 95% contour could not be achieved, the full reference bandwidth value

was used. This allowed areas of use that were genuinely disjunct to remain, and was used in preference to applying a value greater than 1.0 of the reference bandwidth, which would have resulted in considerable oversmoothing of the home range. Home range kernels were produced in ArcGIS 9.2 using HRT: Home Range Tools for ArcGIS (Rodgers et al., 2007). A raster cell size of 30m was used. MCPs were also produced to allow direct comparison of home range size with the radio-tracking study by Gray et al. (2009).

Home range sizes were compared between the entire dry season and the core breeding period using paired t-tests, and between sexes using independent samples t-tests. For individuals with multi-year data, home range size was averaged across years to avoid pseudoreplication. Home range areas (95% kernels, 50% kernels and MCPs) were log-transformed prior to analysis, to give normal distributions and equal variances. Statistical tests were performed in SPSS 16.0. The effect size (r) is reported along with p values. With small sample sizes there may be insufficient power to reject the null hypothesis, and so reporting the effect size is particularly useful for interpreting the results in this situation (Gliner et al., 2001). The first two seasons of individuals (one male and one female) tagged as subadults were excluded from these analyses (but are presented in the maps). Whether individuals that have larger home range in one year also have large home range in subsequent years was examined by correlating first and second season home range area.

Site fidelity

Inter-annual site fidelity was assessed by the percentage of an individual's first dry season tracked home range that was overlapped by each of the following seasons' home ranges. For each individual tracked for more than two seasons, the mean overlap was calculated to avoid pseudoreplication. Site fidelity was compared between adult males and females by an independent samples t-test. Subadults were excluded from this analysis.

Habitat selection

Home range kernels were overlaid on a habitat map from February 2009, produced by supervised classification of a LANDSAT image (see Chapter 2 for details and methods). Habitat composition of 50% and 95% home range kernels for the core breeding period were extracted

from the habitat map. For individuals with multiple seasons of >24 locations, the average habitat composition of the home range kernels was used. Habitat availability for the study area was determined by the habitat composition of the Minimum Convex Polygon enclosing all breeding season locations, buffered by the mean radius of the 95% kernels. Compositional analysis (Aebischer et al., 1993) was used to determine habitats selected and avoided. See Chapter 4 for more details of the methods used to assess home range kernel habitat selection from remotely sensed data. The possible relationship between home range size and habitat quality was examined by correlating home range size and percentage grassland cover of the home range (both square root transformed to reduce leverage).

Results

Timing of breeding

Thirty nests were reported from the four breeding seasons from 2008 to mid-July 2011. Nest reports ranged from March to August, peaking in April and May, with lower numbers in June and July (Figure 1). As clutches may have been laid up to 25–28 days prior to being found, this suggests clutch initiation potentially varied between February to August, peaking during March to May. Dry season rainfall increased in April, peaking in May (in 2008 and 2009) and June (in 2010). In 2010 rainfall remained high in July and August, compared to the two previous years, coinciding with some late season nest reports.

Home range extent and patterns

Home ranges were consistently larger for the whole dry season (December–August) than in the core breeding period (mid-February–early June), whether considered as 50% kernels (paired t test: t_{19} = 2.180, p = 0.042, r = 0.45), 95% kernels (t_{19} = 3.085, p = 0.006, r = 0.58) or MCPs (t_{19} = 4.715, p < 0.001, r = 0.73); see Table 2 A and B. Home range area use across the entire dry season was expanded by areas used early (e.g. Figure 2 E) and late (e.g. Figure 2 B) in the season; most outlying locations were also from these periods. Where home ranges were multimodal (consisting of more than one 50% core), the modes were generally occupied during different periods of the dry season (e.g. Figure 2 A).

For the whole dry season, individual's home range area (95% kernel) was positively correlated between first and second seasons (Pearson Correlation, $r = 0.814$, $p < 0.001$, Figure 3).

Home range 50% kernels of females were marginally larger than those of males ($t_{19} = -1.904$, $p = 0.072$, $r = 0.40$, Table 2 A) but their 95% home range kernels and MCPs were similar (former $t_{19} = -0.607$, $p = 0.551$, $r = 0.14$; latter $t_{19} = -0.841$, $p = 0.411$, $r = 0.19$). For MCPs this may be due to large variance in female extent that masked an apparent trend for larger home range area compared to males. For the core breeding period, female core 50% kernel home ranges were again larger than those of males ($t_{18} = -2.024$, $p = 0.058$), with a medium-sized effect, $r = 0.43$ (Table 2 B). Again, both sexes had similar-sized 95% kernel home ranges ($t_{18} = -0.817$, $p = 0.424$, $r = 0.19$) and MCPs ($t_{18} = 0.115$, $p = 0.910$, $r = 0.03$). Home ranges (50% and 95% kernels and MCPs for the core period) were an order of magnitude larger than those found by Gray *et al.* (2009) using radio-tracking.

For the subadult male tracked, breeding period home range was very large in the first season compared to adult males, and subsequently decreased in size substantially each year for both the 50% core kernel (13.8 km^2 in 2008, 4.3 km^2 in 2009, 1.0 km^2 in 2010 and 0.2 km^2 in 2011) and the 95% outer kernel (112.9 km^2 in 2008, 47.3 km^2 in 2000, 7.9 km^2 in 2010 and 4.5 km^2 in 2011). In contrast, the subadult female's home range size was much smaller, in keeping with adult female home range size, and remained quite constant (50% kernel: 2.8 km^2 in 2009, 5.0 km^2 in 2010 and 3.3 km^2 in 2011; 95% kernel: 28.6 km^2 in 2009, 29.0 km^2 in 2010 and 27.7 km^2 in 2011).
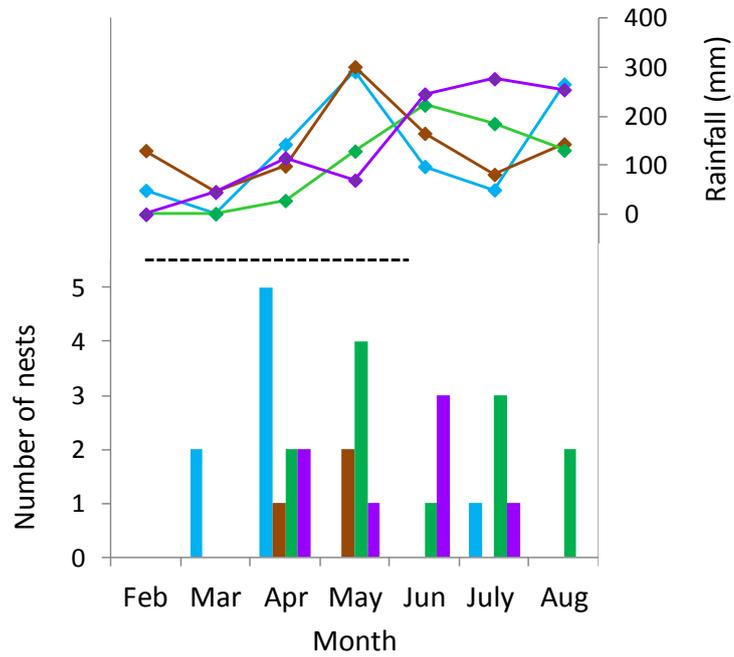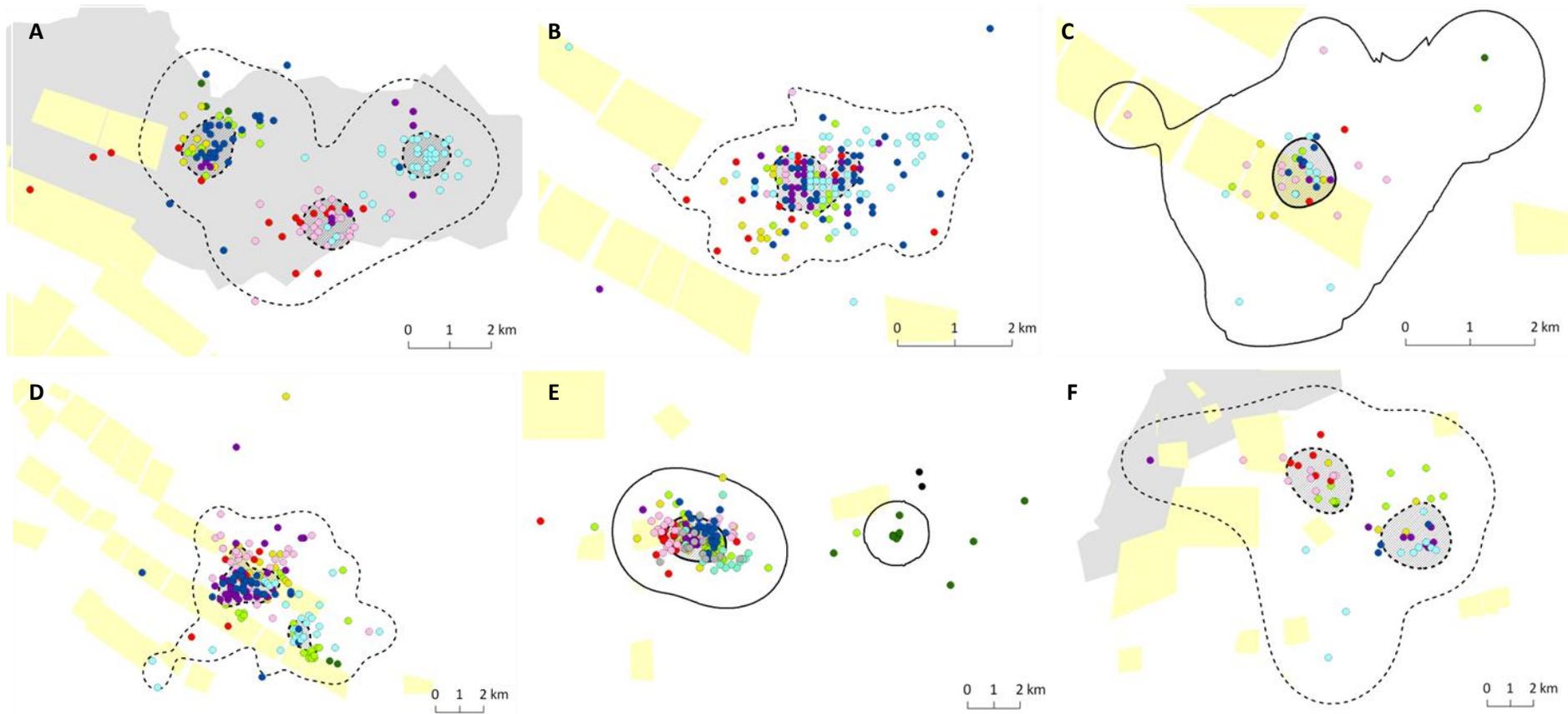
Figure 1. Number of nests (with eggs) reported and rainfall by month for 2008 (blue), 2009 (brown), 2010 (green) and 2011 (purple). Nest reports up to 17/07/11. Black dashed line indicates period of male display activity (from Davidson, 2004).

Table 2. Mean (± SE) and range of adult male and female home range areas (95% kernels and MCPs) and core areas (50% kernels) for the whole dry season (A; December–August) and for the core breeding period (B; mid-February–early June, with results from the radio tracking study of Gray *et al.* (2009) shown in square brackets).

A	Home range area (km^2)								
	50% kernel core			95% outer kernel			MCP		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Males (*n* = 12)	2.6 ± 0.9	0.7	11.1	31.3 ± 8.5	8.4	92.6	39.2 ± 9.7	5.9	108.5
Females (*n* = 9)	4.7 ± 1.6	1.1	17.3	42.8 ± 17.6	8.4	180.3	121.6 ± 78.9	7.4	738.7
All (*n* = 21)	3.5 ± 0.9			36.2 ± 8.8			74.5 ± 34.3		

B	Home range area (km^2)								
	50% kernel core			95% outer kernel			MCP		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Males (*n* = 12)	1.6 ± 0.3	0.5	3.5	22.1 ± 4.7	5.5	55.0	23.4 ± 6.1	3.5	73.3
[*n* = 8]	[0.2 ± 0.1]	[0.03]	[0.4]	[1.6 ± 0.4]	[0.4]	[3.5]	[2.5 ± 0.6]	[0.4]	[5.1]
Females (*n* = 8)	3.6 ± 1.1	0.8	9.5	36.8 ± 15.7	6.4	141.6	27.4 ± 14.1	4.1	123.8
[*n* = 5]	[0.8 ± 0.2]	[0.4]	[1.8]	[6.2 ± 1.7]	[2.2]	[12.0]	[6.7 ± 1.1]	[2.4]	[8.9]
All (*n* = 20)	2.4 ± 0.5			28.0 ± 6.8			25.0 ± 6.5		

Figure 2. Dry season home ranges with outer 95% and core 50% (shaded) kernels for two male (solid line) and four female (dashed line) floricans. Locations are coloured by month and overlain on BFCAs (grey shading) and dams/headponds (yellow shading).

Location month

Early season	Core season	Late season
● November	● February	● June
● December	● March	● July
● January	● April	● August
	● May	
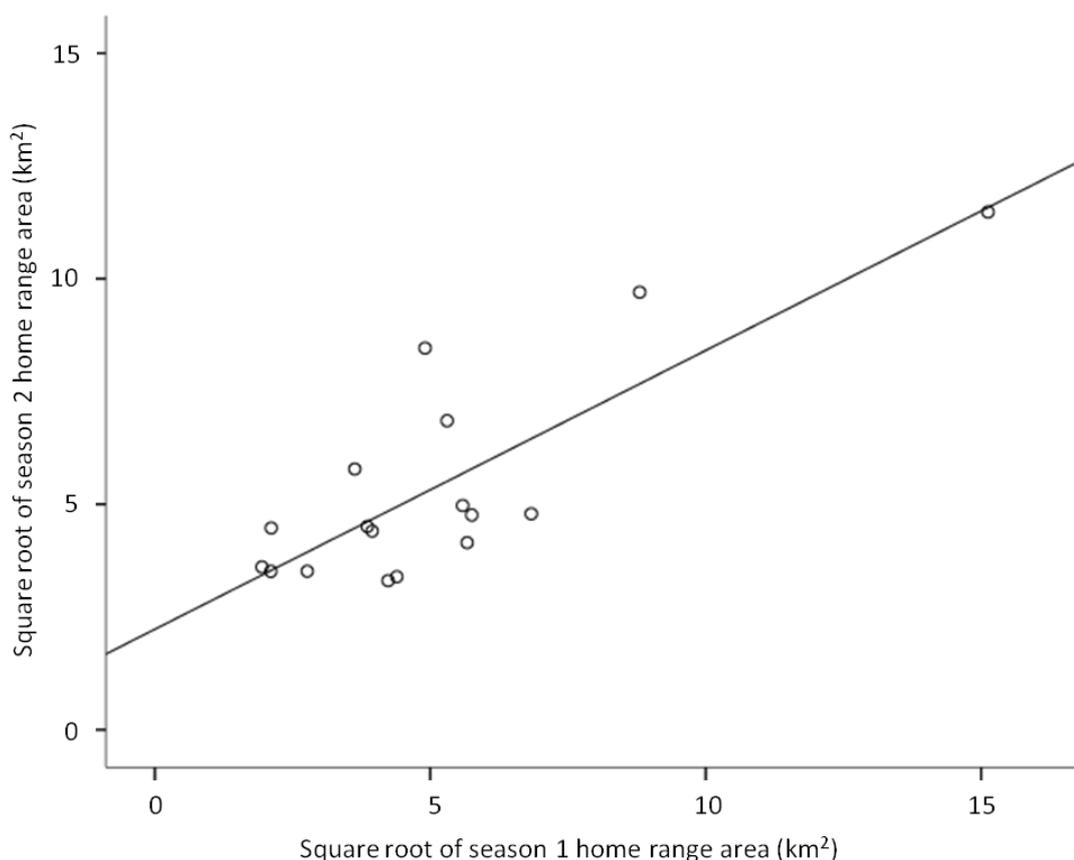
Figure 3. Home range size (95% kernels for the whole dry season period) in seasons one and two for each individual with multiple season data (n = 17). The first two seasons (in relation to the year of tagging) were used for all individuals except two sub-adults, for which later seasons were used to ensure adult home ranges only were included.

Home range overlap between individuals

There was considerable overlap of breeding period 95% home range areas of tagged birds, both between and within the sexes (Figure 4). In contrast, overlap of 50% core areas was limited, only occurring to any substantial degree in three instances, each time between a male and female(s): in 2011, a male 50% core completely covered a female 50% core (with temporal overlap in locations) and partially covered a second female's 50% core area (no temporal overlap: Figure 4 A) and in 2010, a male 50% core entirely encompassed a female's 50% core (with temporal overlap in locations: Figure 4 B). In areas where BFCAs have been established, individual home ranges reached far beyond the protected areas and were large relative to the total BFCA extent. Pooling home ranges from all years, 31% of male home ranges were multimodal, compared to 53% of female home ranges (and some individuals switched between uni- and multimodal home ranges in different years). The subadult male had an

unusual home range in the first season (Figure 4 E, 2008), being very large and consisting of five separate core areas. In the second season, two separate (95% kernel) areas were occupied (Figure 4 E, 2009). One other florican, an adult male, also occupied two disconnected 95% kernel areas (Figure 4 D, 2011).

Inter-annual site fidelity

Floricans tracked over multiple seasons were found to show strong fidelity to their breeding areas. The 95% kernel home ranges of all individuals overlapped with their first season home range in every subsequent season monitored. Average inter-annual overlap in 95% home range kernels was 59% (SE = 7.9) for ten adult males and 61% (SE = 7.5) for seven adult females, with no difference in the degree of site fidelity between the sexes (t_{15} = -0.217, p = 0.831, r = 0.06). Two subadults (included as adults above for their final two seasons monitored) also exhibited site fidelity between their first and second seasons, with an overlap of 41% for the male and 81% for the female.

A. STOUNG-CHIKRENG

2008

2009

2010

2011

Habitat Legend
- Wet grassland
- Dry grassland
- Scrub
- Wet season rice
- Dry season rice
- Wetland

0   5 km

B. SAN KOR

2008

2009

2010

2011

0   5 km

N

106

C. KROUS KRAOM 2010 N

2011

0 5 km

D. CHONG DONG 2010

2011

E. BARAY

2008

2009

2010

2011

0   5 km
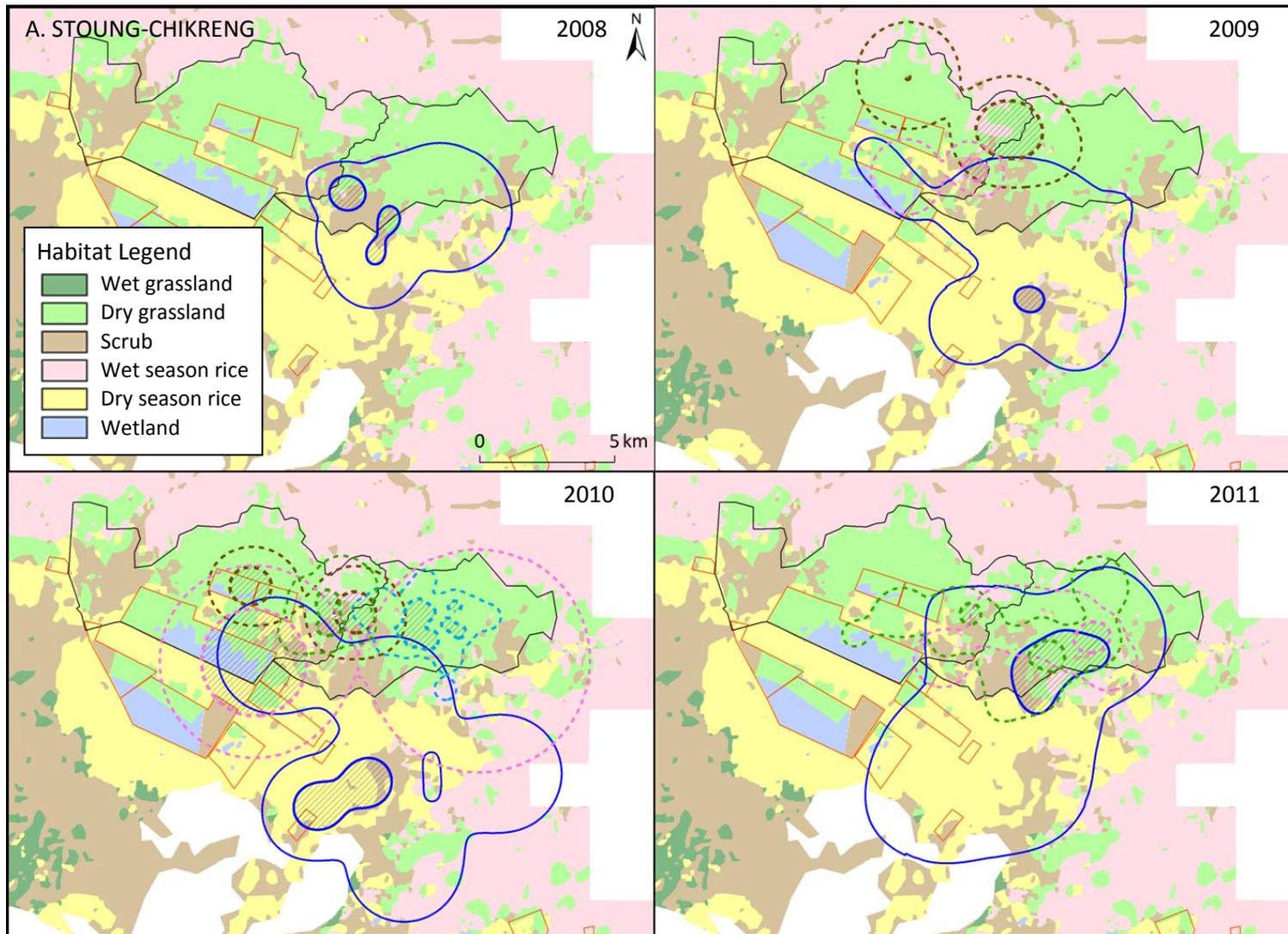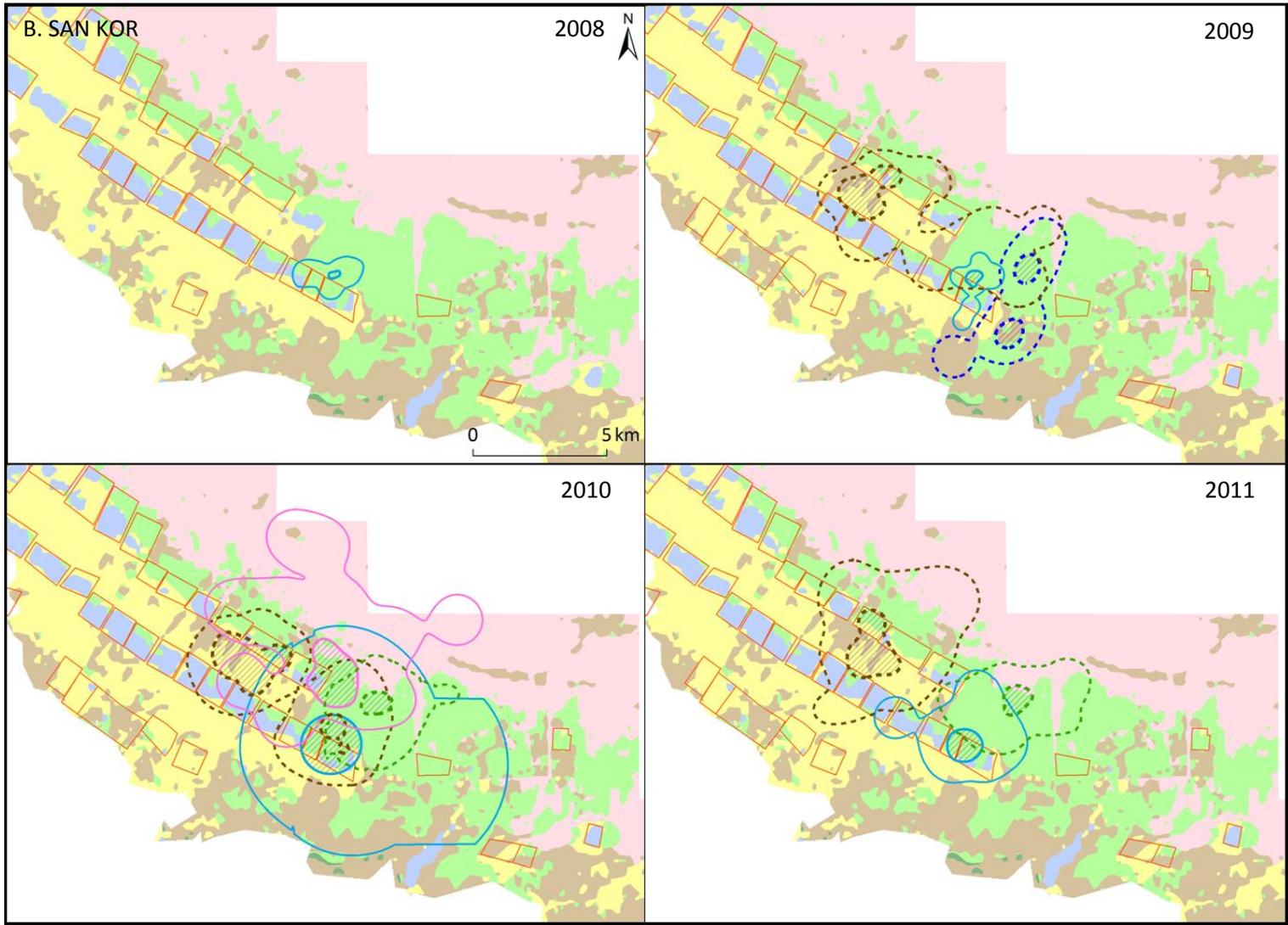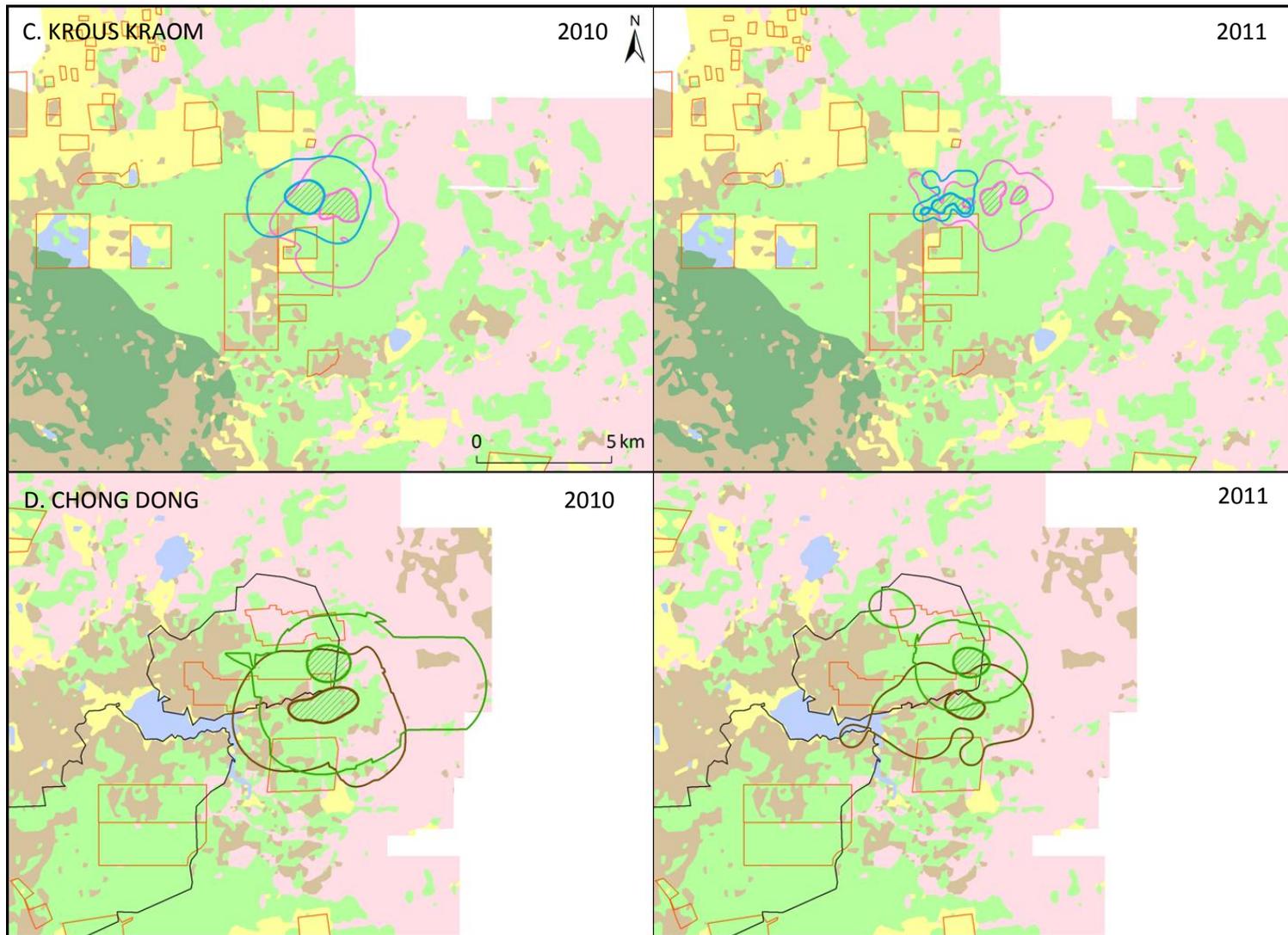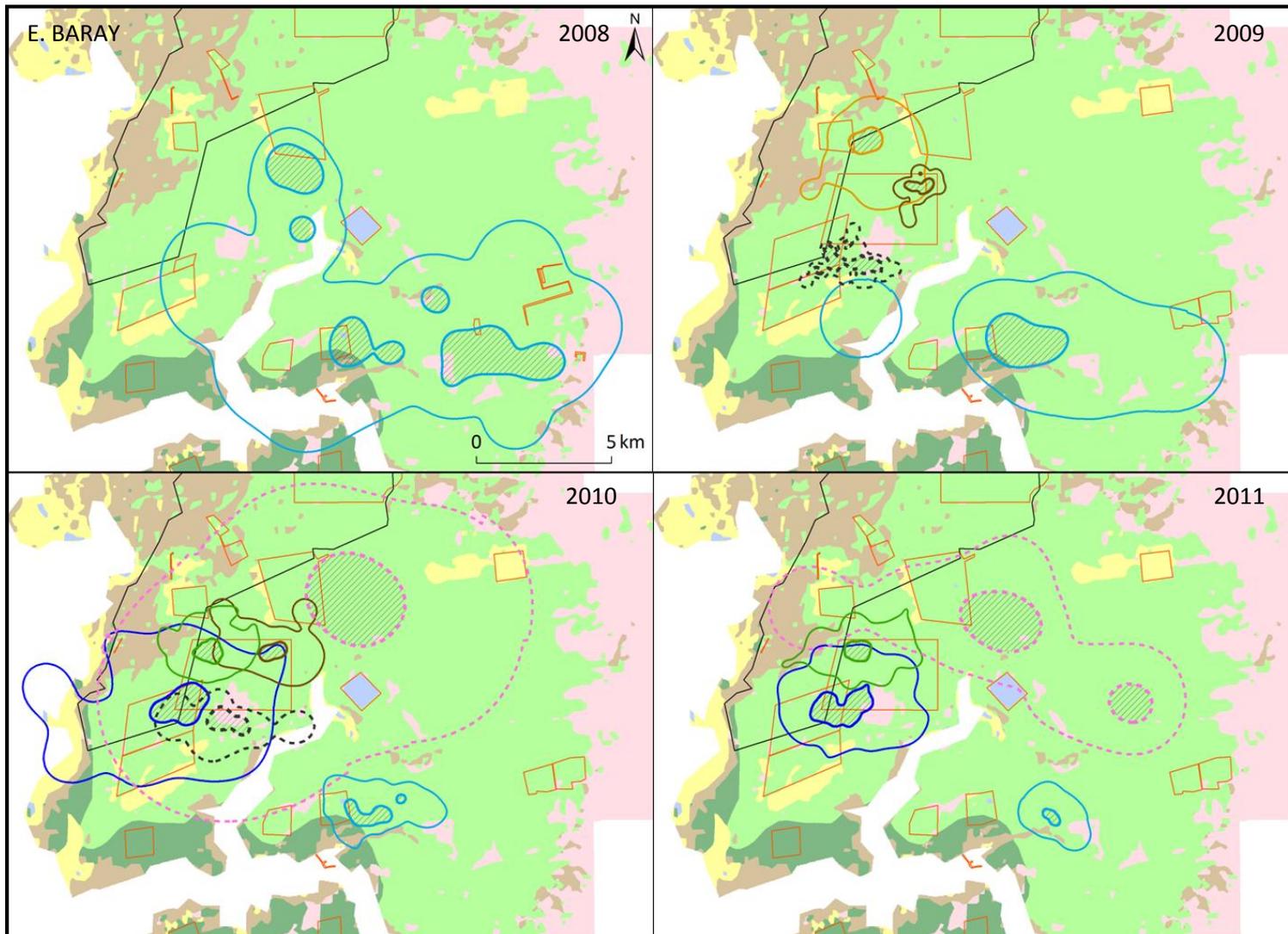
Figure 4. Home ranges (95% outer kernels with 50% cores, shaded) for the main breeding period at the five study sites: Stoung-Chikreng, San Kor, Krous Kraom, Chong Dong and Baray, 2008–2011. For each site, different colours indicate different individual floricans; the same colour between years indicates the same individual; solid lines indicate males, dashed lines females. Home ranges are overlain on a habitat map (see legend for habitat types) with BFCAs (black outline) and dams/headponds (orange outline, updated for each year except 2011, where 2010 dam locations are shown).

Home range habitat use

Habitat availability within the breeding season study area consisted mostly of grassland, followed by wet season rice, scrub and dry season rice. Wetland was only a minor component of the study area (Table 3). Compositional analysis showed only grassland to be positively selected, and significantly more so than any other habitat type (95% kernel habitat: GRL>>>SCR>WSR>DSR>WTL, 50% kernel habitat: GRL>>>WSR>WTL>SCR>DSR, Figure 5). Avoidance of all other habitat classes was more pronounced for 50% than 95% kernels. Home ranges that comprised a greater proportion of grassland were smaller (Spearman's rho, $r = -0.681$, $p = 0.001$, Figure 6).

Table 3. Habitat availability for florican breeding areas.

Habitat	Area km^2 (percent composition)
Grassland (GRL)	700 (35)
Scrub (SCR)	430 (21)
Wet season rice (WSR)	543 (27)
Dry season rice (DSR)	312 (15)
Wetland (WTL)	46 (2)
Total area	2031
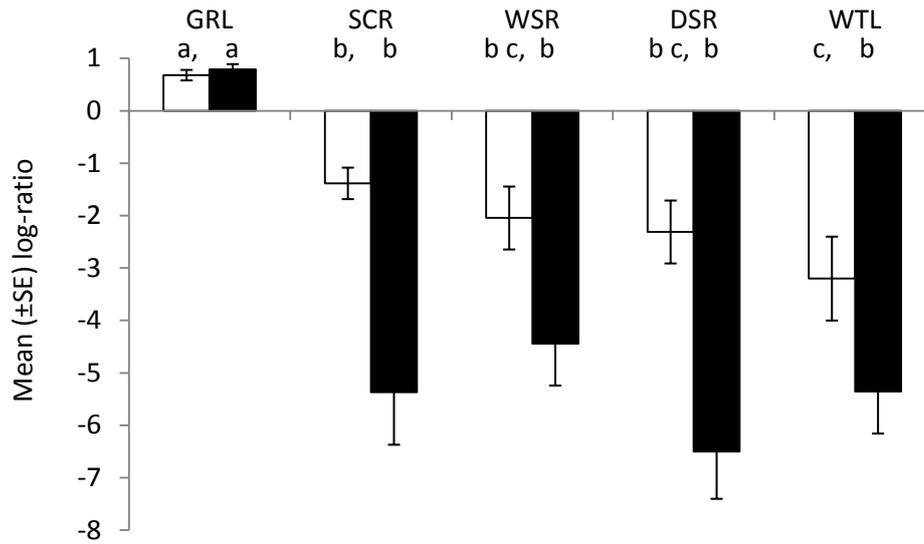
Figure 5. Mean (± SE) log-ratios of used/available habitat for 95% (hollow bars) and 50% (solid bars) home range kernels for 21 floricans during the core breeding period (2008-2011). Letters indicate significant differences between habitats, for 95% followed by 50% kernels.

Figure 6. Home range size (95% kernels for the core breeding period) in relation to percentage cover of grassland for 20 individuals.

Discussion

Areas used by floricans during the early and late dry season have not previously been studied, with the focus falling on the core breeding period (mid-February to early June), when sit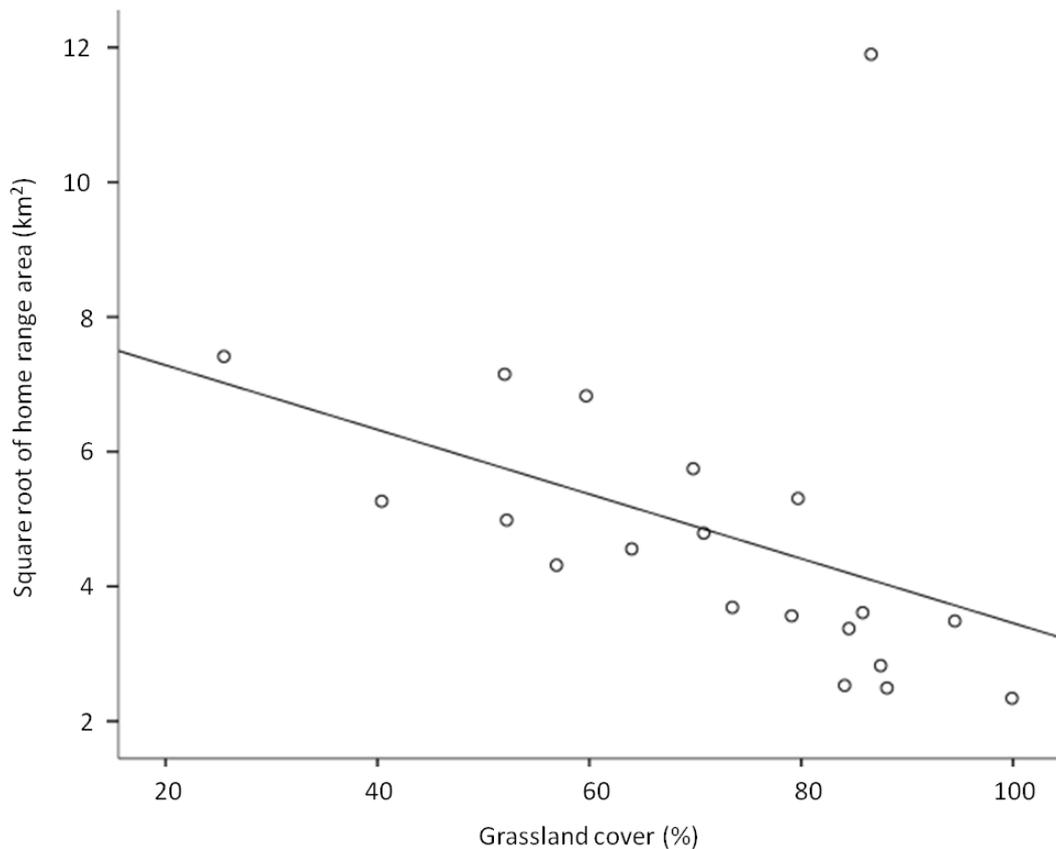es are sufficiently dry to access. On their arrival on the breeding grounds prior to the display/nesting period, floricans often used areas outside of those occupied during the core breeding season. The priority at this time is likely to be access to a good food supply, with birds needing to improve their condition prior to breeding. At the end of the breeding season there were also some shifts in space use, probably in response to flooding, as the breeding grounds are encroached by rising water levels and birds were forced to move away from the lake.

Core breeding period home ranges of satellite-tagged adults were found to be an order of magnitude larger than those estimated by radio-tracking for the same time-period (by Gray et al., 2009). Kernel home ranges for the satellite-tagged birds could have been enlarged by the use of an ad hoc smoothing factor, with this approach tending to over-smooth in comparison to least squares cross validation (LSCV, used in the radio-tracking study), which often under-smooths. LSCV was discarded from this study as it considerably under-smoothed the home ranges, creating highly fragmented 95% kernels with many islands that did not satisfactorily represent the complete area considered to be important for an individual. Another factor which could have resulted in larger home ranges for the satellite-tagged birds is the level of location error. The mean error (calculated from the mid-point of the error classes multiplied by the number of fixes for each class) from satellite fixes was 225m (SD 143), compared to a mean error of 113m (SD 50) reported by Gray et al. (2009). The mean error is trivial when compared to the mean 95% kernel diameter for the core breeding period (5,971m). Taking these factors into account, the difference in home range area is so substantial that a genuine difference seems evident. Furthermore, MCP home range estimates, which are more directly comparable (with an identical method of construction) than the kernels, produced male home ranges nine times larger and female home ranges four times larger than those of Gray et al.'s radio-tagged birds. The larger home ranges of the satellite-tagged floricans are likely to be due to their use of outlying locations beyond the range of radio telemetry. Potential influx of birds from neighbouring areas where habitat has been lost, as well as a deterioration in habitat quality (with expansion of dry season rice and scrub encroachment both perforating grasslands, and potentially increasing disturbance), could also have led to larger home range sizes. In addition, satellite fixes were taken from a range of times during the 24hr period, whereas radio-

telemetry was conducted early morning and late afternoon only (during the period of greatest activity).

The larger home ranges presented here have implications for the amount of land that needs to be protected to support a population of floricans. For example Stoung-Chikreng BFCA is 75 km^2, with 95% kernel home ranges for the whole dry season averaging 31 km^2 for males and 43 km^2 for females, although core areas were considerably smaller (1.6 km^2 and 3.6 km^2 respectively). Whilst the core breeding period home ranges of different individuals showed extensive overlap when considered in terms of 95% kernels, 50% kernels of males were not found to overlap. There was only very slight overlap between females of 50% kernels, although there could well have been many further instances of overlap involving untagged birds for both sexes. However, Gray et al. (2009) found male 95% kernels to be mutually exclusive, whilst females overlapped considerably with each other, as well as with males. The large size of home ranges relative to the BFCAs and possible limited overlap between individuals of 50% cores would suggest that the current resource of BFCAs is likely to be insufficient and unable to sustain a viable population of breeding floricans in the long term.

Our findings have implications for the monitoring strategy used to assess population numbers, which is based on assessing occupancy of displaying territorial males in 1 km squares (each separated by an unsurveyed 1 km square). The method assumes that the males remain within their territories and are likely to be detected during the peak period of conspicuous display behaviour (March–April) when the monitoring is conducted, and will not be counted displaying in more than one square. Repeat visits are made to survey squares to assess detectability and improve estimates. Whilst we have found their movements to be much more extensive than previously thought, it is not known if males displayed in multiple areas of the 95% kernel, or only in a specific core area. Even so, seven of the 12 males had a multimodal home range in at least one season and 50% cores ranged in size up to 3.5 km^2, which would extend beyond a 1 km square area, potentially causing the same male to be recorded in more than one survey square, and resulting in an over-estimate of the population. Alternatively, multimodal cores and large home ranges could be indicative of subordinate males that do not hold a clearly defined or fixed territory. The findings from the subadult male would support this hypothesis, as its first season home range was very large and consisted of multiple cores, suggestive of a bird prospecting for a territory. Subsequent seasons showed shrinkage of the home range and consolidation of a single core area. This is further supported by the observation that the four

males known to exhibit territorial display behaviour (observed prior to tagging) had unimodal home ranges.

Therefore males with multimodal cores could be using a different mating strategy. Without a fixed territory these 'floaters' may behave submissively around other males, resulting in them being tolerated in the territories of others and gaining 'sneak' copulations. This has been observed in another lekking species, the ruff *Philomachus pugnax*, where the strategy is believed to be a low-cost, low-benefit alternative, but one which may result in similar lifetime reproductive success as for territorial males (Widemo, 1998). If this reproductive strategy does occur in the florican population then, contrary to the statement above, monitoring based on territorial displaying males could instead underestimate numbers. If it is assumed that the proportion of territory holders and floaters in the population remains fairly constant, then monitoring should at least show any relative changes in abundance. However, it is likely that these proportions will vary with overall density (with more floaters expected if the density of males increases) and potentially also with habitat quality. In order to assess the reliability of the current monitoring method, it is important to determine whether males display in only a small (<1 km^2) part of their core territory area (males are frequently observed displaying at the same location within their territory, pers. obs.), or more widely (>1 km^2) throughout their home range (in which case the current monitoring method may not be appropriate).

The 50% kernels of three satellite-tagged females overlapped with those of satellite-tagged males, showing that they used core areas of male territories and could have nested within these areas. Gray *et al.* (2009) suggested that females may leave the exploded lek, as three out of six radio-tagged females could not be located for part of the breeding season. However, none of the nine satellite-tagged females left the broad exploded lek area (all had 95% kernel overlap with males), but for part of the season a number of them did shift their cores to a different part of the exploded lek, to areas potentially out of range of radio-telemetry. While this does not exclude the hotshot model of lek evolution, it does provide evidence consistent with the hypothesis that male display territories are aggregated in areas preferred by females, and in which encounter rates with females are high (as for houbara: Hingrat et al., 2008). Multimodal cores were common for females and their occupation during different periods of the dry season suggests that the modes could be related to separate nesting attempts (with the first attempt having failed). A similar pattern of female space use (multimodal home ranges and overlap with the smaller home ranges of males) has been reported in houbara (Hingrat et al., 2004). We speculate that females with unimodal cores may have had nesting

success and remained in the area, unable to move far with dependent flightless chicks. Gray et al. (2009) found that the two females with chicks did not move more than 1.5 km from the nest.

This is the first time that a subadult female has been tracked. The home range was similar to that of adult females and in contrast to that of the wider-ranging subadult male. Adult females had larger core 50% kernels than males, just over twice the size for the core breeding period. Females may require larger areas for foraging with chicks and, unlike the males, are not restricted to a display arena and defined territory. The nest reports suggest that the timing of egg-laying may be linked to mid-season rains, when the parched land is rehydrated and insect abundance (with grasshoppers thought to be a key prey item) likely to peak, providing plentiful food for chicks. In addition, extensive burning, which takes place early in the breeding season (February–March) when the land is very dry, is no longer prevalent and therefore not a risk to nests. The earliest nest report was from 4 March, the latest 9 August, two months after the end of the male display period (although the eggs could have been laid anytime since 12 July). This suggests that either some late matings occur after display activity has ceased, or females make use of sperm storage for late nesting attempts. For houbara bustards used in captive breeding, genotyping of paternity relative to timing of matings showed that females were able to store viable sperm for up to 22 days (Saint Jalme et al., 1994), but more recently this has been found to be up to 50 days (Loïc Lesobre pers. comm.).

Contrary to Gray et al. (2009), who found that females showed weaker site fidelity, in this study males and females exhibited equally strong inter-annual site fidelity in all years tracked, even in areas of substantial habitat change and disturbance (most notably as has occurred at San Kor during the period of this study). This suggests a strong degree of lek inertia even in response to detrimental landuse change, so-called 'ghosts of habitats past' that can occur in long-lived species with strong site fidelity (Wiens and Rotenberry, 1985; Knick and Rotenberry, 2000). It is also interesting to note that in addition to site fidelity, individual floricans tend to hold similar-sized home ranges each year.

Home range size varied considerably between individuals. This is likely to relate to habitat quality; floricans were found to only select grassland, and home range area was greater with decreasing percentage grassland cover. Smaller home ranges are likely to result from better habitat quality, whilst in areas of less suitable habitat, larger home ranges are required to support an individual (as found for some other bird species e.g. Newton 1986). Agricultural

covers (wet and dry season rice), scrub and wetland (which is likely to increase with the expansion of dams and irrigation channels for dry season rice) were all avoided by floricans and as habitat quality deteriorates, florican are likely to require larger areas of land to meet their needs. Gray et al. (2009) also reported strong avoidance of dry season rice fields by males and females, although females did make use of headponds (where unburned grassland remains, as at Stoung-Chikreng). Some female home range cores in the current study overlapped headponds of this type, whilst for males this only seemed to occur more recently (in 2010 and 2011) in areas of extensive dam developments, where there may be little alternative but to use dam areas. Whilst headponds may hold longer, unburnt grassland, favoured by females (Gray et al., 2009), some hold reservoirs of water and others contain irrigated and flooded dry season rice fields, the latter two being completely unsuitable for floricans. The lack of mobility shown by the floricans is worrying in view of the rapid and dramatic habitat conversion that is taking place (see Chapter 2), with the likelihood of subpopulations being able to survive long-term in such inhospitable areas seemingly very poor. Yet there may be few alternative areas of suitable habitat remaining, and in those areas the florican density may already be high, as at Stoung-Chikreng where it has apparently increased in recent years (van Zalinge et al., 2010), potentially rendering the area unable to support additional birds. This may be particularly problematic for males, as they would probably struggle to establish new territories in traditionally occupied areas.

A better understanding of female nesting outcomes and nest and brood rearing habitat requirements is needed, and may be achievable in the future with the use of radio-satellite combination tags (allowing the broad area of occupation to be known from satellite fixes and subsequent real-time radio-tracking to locate nests with accuracy), although considerable caution should be used as the risk of abandonment due to disturbance at the nest could be high. Establishing how food resources are distributed and change throughout the season (also in relation to rainfall) would be useful to investigate further. Protecting exploded leks would appear to be appropriate for both male and female spatial requirements, as females remained within these broad areas. Improving estimates of the number of floricans that can be supported within the areas currently protected as BFCAs will provide important information for assessing the future viability of the population. Consideration should be given to how management (such as scrub removal and facilitating areas currently under cultivation to revert back to grassland) can be used to improve habitat suitability within the BFCAs so that the maximum number of birds can be supported (with each individual requiring a smaller home range area if grassland cover is high). Ensuring strong protection of current BFCAs against dry

season rice developments and, if possible, extending the areas under protection to a size more appropriate given the spatial requirements of individuals must be priorities for the conservation of floricans in Cambodia.

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Chapter 6: Conclusions

Introduction: key findings

This thesis has sought to improve understanding of seasonal landscape use, as well as how the landscape is changing, for Bengal floricans in Cambodia. The rate of loss of key breeding grassland areas has accelerated, driven by commercial dry season rice developments (Chapter 2). Satellite-tracking has revealed the movements and areas occupied by floricans during the non-breeding season, of which very little was previously known, as well as differential use of non-breeding areas by birds from the northern three and southern two sites (Chapter 3). It has also been shown that, if sufficiently dry, floricans will remain in the breeding grasslands throughout the wet season, suggesting that flooding of their habitat is the cue to migrate. Wet season habitat requirements are now better understood (with florican preferring open savanna and grassland), as well as the different availability of habitats and threats faced by birds in the northern and southern areas of the total study site (Chapter 4). Use of the grasslands pre- and post-breeding shows a wider area of occupation than found during the core breeding period (Chapter 5). For the core breeding period, home ranges were found to be an order of magnitude larger than previously thought. Whilst all females were found to remain within the exploded lek, contrary to what was suspected from a radio-tracking study by Gray et al. (2009), many shifted their positions to a different part of the home range for the latter half of the season.

This concluding chapter will consider the benefits and constraints of using remotely sensed data, a key element in this thesis, to address conservation questions. The conservation implications of the findings presented here, along with the recommendations that flow from them, will be discussed in terms of broad approaches as well more specifically for breeding and non-breeding areas. Research questions that still remain to be addressed are also considered.

Mapping habitats from satellite images

In this thesis, the use of remotely sensed data, combined with ground-truth training points, enabled the production of an up-to-date landcover map both for the outer floodplain area of interest, to assess rates of grassland conversion (Chapter 2), and for the florican non-breeding areas, to which satellite location fixes could be related in order to assess habitat preferences (Chapter 4). For both areas, achieving sufficient classification accuracy was important to ensure that meaningful conclusions could be drawn from them. The error in the classifications

and relatively coarse resolution represented a limit to the accuracy and level of detail that could be achieved, but enabled large-scale habitat information to be obtained that would have otherwise required prohibitively time-consuming and expensive alternatives (such as field-based mapping or aerial photography). The non-breeding habitat map allowed coarse-resolution habitat selection to be assessed, which was also backed up by field-based measures to assess finer-scale preferences. The map also enabled the identification of areas of potential suitable florican non-breeding habitat (areas classified as open savanna and medium forest) that have not previously been searched on the ground and therefore can provide a means to focus future ground surveys efficiently.

Using satellite transmitters to track movements and assess habitat preferences

Use of satellite telemetry

The use of satellite telemetry has improved understanding of florican wet season areas, habitat requirements and threats. Unlike radio telemetry, satellite transmitters do not require detection in the field, thereby saving significant time and resources, and rapidly paying back in accumulating scientific data the substantial financial outlay for the equipment and downloads. They also enable long-distance movements and individuals that travel to unknown or inaccessible locations to be tracked, a clear advantage over conventional radio telemetry, which can only track movements over distances far shorter than many migrant bird species travel. The accuracy of locations provided by satellite transmitters has also improved considerably, with GPS transmitters giving locations of <100m error radius. As the accuracy of GPS technology improves, the opportunity to relate locations to finer-scale habitat variables becomes possible. Satellite-tracking can also be less biased than radio-tracking, by providing fixes from inaccessible areas as well as from unexpected distant locations, both of which are likely to be missed by radio telemetry. Therefore satellite telemetry studies often show animal movements to be much more extensive than those using more traditional methods (Hebblewhite and Haydon, 2010), as was found in this study for the breeding home ranges of male and female floricans. In addition, sampling locations at regular intervals, thereby reducing spatial and temporal correlation between points, is much more feasible with satellite telemetry. In this study, the first to track the movements of the Bengal florican outside the breeding season anywhere in its range, satellite telemetry has identified areas occupied during the non-breeding season and thereby enabled habitat use to be determined, which was not previously possible with radio telemetry owing to the large potential area available to birds,

the lack of knowledge of potential areas to search, and access difficulties due to wet season flooding (see Chapter 3).

The majority of transmitters deployed in this study were Argos rather than GPS units. GPS units deployed on males appeared to perform well initially (as can be seen in Table 1 for the first three months) but there was considerable variation between the units, and fixes were generally highly temporally clumped (e.g. logged every hour for a day and then a large gap before the next fixes were obtained), and over time delivery became very sporadic and occasional. The poor performance of the GPS units was related to low power generated by the solar panels, as the GPS element has higher power demands than are required to obtain Argos fixes. This may seem surprising in a tropical country which experiences intense sunshine, but the tendency of floricans to take cover for long periods in vegetation, reducing charging opportunity, as well as feathers potentially covering the solar panel, are likely to have contributed to the low power of these units. This problem was exacerbated in the wet season, when charging conditions were worse due to overcast conditions, greater vegetation cover and potentially even more skulking behaviour. Units deployed in the following year on females, with a more conservative duty cycle deliberately programmed, provided scarcely any fixes during the breeding season (Table 1), probably because the females were concealed in vegetation for much of the day whilst nesting, such that units received insufficient sunlight to meet their high power demands. Consequently Argos-only units were trialled in the second season of transmitter deployment and, proving much more reliable (providing locations at greater temporal frequency and with substantially less variation between units), were used exclusively in the third season. Interestingly, solar units deployed on subadults (one GPS unit on a male and one Argos unit on a female) performed a great deal better than those deployed on adults, perhaps because subadults spend more time moving around in the open. The drawback of Argos units was the lower accuracy location fixes (at best < 250 m, compared to GPS < 100 m).

Duty cycles specified for battery units are a trade-off between the frequency of location fixes and the desired duration of the transmitter lifespan. For solar units, the trade-off involves obtaining as many locations as can be powered by the solar panels, without running out of charge (which would result in periods of time when no locations are received until the unit has had the opportunity to re-charge). For this study, multi-year data were required (to understand annual movement patterns, determine site fidelity and estimate survival) but it was also important to obtain, first, locations often enough to know with some accuracy when

movements occur and, second, a sufficient number of fixes to allow accurate generation of home range kernels within a season. The considerable effort and inherent risk involved in catching individuals (see Appendix), along with the cost of the units, the use of permanent attachment and the longevity of the birds, meant that using multi-year (solar-powered) transmitters was preferable (to battery-powered units) and better justified.

Whilst there were no negative impacts observed of the harness-mounted transmitters used on floricans, there is little information to be certain that this was the case. Birds were observed immediately after release, but other than that they were rarely re-sighted in the field, so assessing impacts was difficult. Movement data from the transmitters have shown that survival rates of the tagged birds were high and that they were capable of successful return migration (Chapter 3). One individual that was hunted and its body subsequently retrieved was examined for any physical signs of impacts from the transmitter/harness, but none was found and the fit of the harness was still good, six months after deployment (M. Handschuh pers. comm.). However, less obvious impacts that have been reported for other tagged bird species, particularly those with harness-mounted transmitters, include reduced nesting success (Croll et al., 1996; Paquette et al., 1997) and device-induced behaviours such as increased preening (Barron et al., 2010). Such effects would have gone undetected in this study. Clearly these are important issues to consider, along with the potential bias of data from tagged individuals that may not behave normally, yet most studies (including this one) have limited ability to assess these impacts, as obtaining comparable information (on movements and behavioural patterns) for untagged individuals is often difficult and in many situations impossible (Barron et al., 2010). Given the impacts that have been reported for other species, it is important to consider whether the gains in knowledge and information needed for conservation justify the risk to (see Appendix) and potential impacts on individuals, especially when dealing with a very rare species. In this case, study aims were explicitly focused on addressing questions key to the conservation of the species, providing some justification for the risk and potential impacts.

Table 1. Details of satellite transmitters deployed on Bengal floricans in February–March in the years 2008, 2009 and 2010. Performance of transmitters in the first three months (1 April–1 July) of the first year of deployment is shown (when performance was generally best).

Manufacturer	Unit weight	GPS / Argos	Power source	Estimated unit lifespan (years)	Duty cycle	Transmission frequency	Mean 'usable'† locations 1 Apr–1 Jul	Number deployed (and sex)
Microwave Telemetry	45g	GPS & Argos	Solar	3+	2 hr step (0000–2200)	Every day	GPS: 54 (SD 57) LC3: 23 (SD 4) LC2: 27 (SD 2) **TOTAL: 104 (SD 70)**	3 (male inc. 1 subadult)
					3 hr step (0600–1800)	Every 3 days	GPS: 0 LC3: 1 (SD 1) LC2: 3 (SD 2) **TOTAL: 4 (SD 4)**	2 (female)
Microwave Telemetry	35g	Argos	Solar	3+	10 hr on, 24 hr off	Every 3 days	LC3: 22 (SD 15) LC2: 47 (SD 25) **TOTAL: 68 (SD 39)**	11 (6 male, 5 female inc. 1 subadult)
North Star Science & Technology	30g	Argos	Battery	1* (1100 hours on)	8 hr on, 70 hr off	Every 3 days	LC3: 13 (SD 3) LC2: 14 (SD 1) **TOTAL: 27 (SD 3)**	5 (3 male, 2 female)

†Locations of GPS (<100m error radius) and Argos location class 3 (LC3, <250m error) and 2 (LC2, 250–500m error) quality, with locations < 15 minutes apart (autocorrelated) removed. *Duty cycle determined battery life.

Usefulness of radio telemetry and combination tags

The great expense of satellite transmitters, which is compounded by data download costs, is a major constraint on sample size and therefore statistical power (Hebblewhite and Haydon, 2010). Satellite transmitters allow large-scale movements to be tracked and previously unknown sites to be located. The sample size for subsequent more detailed/fine-scale aspects can be increased by supplementing the satellite transmitter sample with much cheaper radio transmitters. As long as sufficient satellite transmitters are deployed to cover the range of areas used by a population, satellite locations can then provide guidance to areas to be targeted for radio-tracking. For habitat studies, it is often not possible to get sufficiently close to radio-tagged individuals to sight them without affecting their behaviour or influencing their movements. Triangulation allows approximate locations to be determined at a distance. With this approach, Grey et al. reported a mean error of radio locations of 113 ± 50m. Mean error (weighted by number of fixes in each accuracy class) in satellite locations in this study was 225 ± 143m. Clearly location fixes with reduced error are most useful when assessing habitat preferences and relating locations to habitat maps. Using buffers around high error locations helps to deal with uncertainty but produces conservative estimates of selection, as unused habitats are also incorporated (Rettie and McLoughlin, 1999; McLoughlin et al., 2002). The higher accuracy achieved by radio compared to satellite techniques for florican tracking to date suggests that there are still aspects of research for which radio transmitters are advantageous. In addition, satellite transmitters have been found to perform less well under dense tree canopy cover, which can bias results towards more open habitats (Cargnelutti et al., 2007; Sager-Fradkin et al., 2007; Heard et al., 2008).

A further disadvantage of satellite units compared to radio telemetry is that they do not provide real-time locations, making it very difficult to locate specific individuals in the field with certainty. Moreover, the poor performance of GPS units (producing very few locations), along with the error of Argos location fixes (at best <250m) and the need for a conservative duty cycle resulting in a location of <250m or 250–500m accuracy being received at best once every few days, meant that locating nests from satellite data was not possible (see Chapter 5). For these situations radio telemetry, despite its decreasing popularity, still has advantages. Gray et al. (2009) were able to locate nests of two out of six female floricans tracked, as radio telemetry allowed accurate pin-pointing of an individual's location. However, three of the six females could not be located for part of the breeding season, possibly having moved some distance to nest, beyond the range of radio telemetry (supported by the findings in Chapter 5).

Therefore making use of the properties of both radio and satellite telemetry with combined tags could greatly improve our understanding of female nesting ecology, as shifts in the home range core area for parts of the season would be detected by satellite locations, allowing guidance of subsequent on-the-ground radio-tracking to locate nests. Furthermore, combination tags would help determine survival outcomes more accurately. For satellite transmitters, when locations cease, it is assumed to be due to tag failure or death (with the transmitter destroyed or in such a position that it can no longer transmit, e.g. buried under soil or water or residing in a hunter's house). For radio transmitters, there is a further option: the bird has moved a distance beyond the range of receivers and a signal cannot be detected. With combined tags, if the satellite element fails, the transmitter may still be located by radio telemetry; if the radio element fails, movements will still be evident from satellite locations; and if a radio signal cannot be detected because the bird has moved far away, this should also be evident. The potential to locate dead individuals or lost tags is also much greater with radio telemetry.

General conservation considerations

Conserving threatened migratory species is particularly challenging, owing to the scale over which movement patterns and habitat associations need to be considered and the potential for a range of threats to be encountered that require different approaches to address. This is true even for a short-distance migrant like the florican. The species faces loss of its grassland habitat, driven by rapid expansion of commercial dry season rice cultivation, in its breeding areas (Chapter 2). In the non-breeding areas, open dry dipterocarp forest habitat is threatened by the spread of plantations (in the north) and in the south there is a lack of suitable habitat owing to extensive agricultural cover (Chapter 4). In addition, the species faces threats from hunting in both breeding and non-breeding areas, the risk appearing to be highest during the wet season (Chapter 3). For the florican to survive in Cambodia, these different threats, occurring in different areas and at different times of the year, will all need to be addressed in a comprehensive conservation strategy. Ignoring threats in the non-breeding areas will almost certainly undermine efforts that have been made in the breeding areas to secure the future of this species.

Implementing effective conservation strategies in developing countries such as Cambodia is a task full of challenges, complications and obstacles that are rarely as problematic in more developed countries. In most developed countries, natural areas and wildlife are valued even

when there is no direct financial benefit. This is a luxury that can be afforded when basic needs such as food, shelter and income are not a serious daily concern. Most developed countries have already lost much of their natural areas and biodiversity, destroyed along the route to achieving development. Therefore it is understandable that the drive for development in countries such as Cambodia is posing the same threat as development that has already taken place elsewhere. But Cambodia still has some large intact natural areas remaining and a rich biodiversity. Is development achievable here without the destruction of its unique ecological assets? Currently this looks doubtful, but there are many different local, national and international organisations working to protect habitats and species and all hope is not yet lost: there is still habitat and biodiversity to conserve. Success will depend on transparent institutions and governance, but also on developing approaches that do not deny the aspiration of local communities to improve their livelihoods.

Conservation strategies must therefore seek to find ways to benefit local communities and engage them in environmental awareness. The Wildlife Conservation Society has established Community Management Committees in florican areas, which collaborate on land management, report illegal activities (such as dam construction and hunting, which can then be dealt with quickly) and provide local guides for ecotourism, generating income from tourist trips (Sum Song, 2009). This creates a direct financial incentive for supporting conservation, but needs to benefit as many members of the communities as possible to gain maximum support.

The most serious threats to florican areas does not come from the local communities, where exploitation of natural resources is much more justified given the extent and severity of human poverty around the Tonle Sap (World Bank, 2006), but from external businessmen and companies seeking to take land for extensive rice cultivation (in breeding areas) or plantations (in non-breeding areas). The benefits of these commercial ventures for local communities are often limited, negative impacts are frequently substantial (e.g. loss of communal land for traditional low-intensity rice cultivation and cattle grazing and exclusion from floodplain fisheries) and therefore both local communities and the environment often suffer. This means that conservation and protecting the livelihoods of local communities can, unusually, be on the same side. Firm action needs to be taken by the government to prevent exploitation by companies. As yet, a lack of political will combined with corruption at every level is probably the greatest obstacle to conservation efforts. Protected areas suffer as 'paper parks', while illegal activity and unlawful developments continue.

The survival of the Bengal florican is heavily dependent on the Cambodian population, which constitutes at least two-thirds of the global population (Gray et al., 2009). The subspecies *H. b. blandini,* occurring in Cambodia, is morphologically distinct (described as having a shorter bill with a heavier base, richer plumage coloration and, in males, shorter ornamental feathers on the head and neck: Delacour, 1929), and it seems very likely to have been separated from the nominotypical form found in India and Nepal for a very long time. Therefore conservation of both populations is clearly important to maintain genetic diversity.

Conservation in breeding areas

Currently, all conservation efforts in the breeding areas are focused on the Bengal Florican Conservation Areas (BFCAs). Twenty nine percent (71 km^2) of the originally designated areas (total area: 244 km^2) are no longer protected, but the remaining areas have received a higher-level conservation status (recognised as areas of national conservation importance by the Ministry for Agriculture, Forestry and Fisheries; van Zalinge et al., 2009). Unfortunately, however, the sizes of florican home ranges revealed by satellite tracking are an order of magnitude larger than those previously established from radio telemetry (Gray et al., 2009), because the outer locations of more distant forays are recorded. Whilst the extent to which floricans overlap in their home ranges is not clear (as only overlap between tagged birds could be assessed in this study), it appears that overlap occurs readily at the 95% kernel level. However, male–male overlap within core (50% kernel) areas seems unlikely given the strong degree of spatial separation in the breeding season (Davidson, 2004), indicative of territoriality, and was not observed between tagged birds (female–female overlap in 50% cores of tagged birds was also not seen). Therefore, whilst we do not know how many floricans can be supported by a certain area, the size of the home ranges alone would suggest that the BFCAs may not be large enough. For example, mean 95% home range kernels were 31 km^2 for males and 43 km^2 for females. The smallest breeding BFCA (Chong Dong) is 26 km^2, the largest (Baray) 73 km^2 (van Zalinge et al., 2009). This concern is made greater by evidence that, in other bustard species, smaller leks are more likely to become extinct (Lane and Alonso, 2001; Alonso et al., 2004; Inchausti and Bretagnolle, 2005; Pinto et al., 2005).

Regrettably, there is very little possibility of extending the BFCAs (T. D. Evans pers. comm.) and therefore efforts must now concentrate on ensuring that the integrity of the current BFCAs is maintained, illegal developments prevented, and habitat suitability maximised so that these

areas can support a high density of floricans. Removal of scrub and preventing further encroachment (by increasing grazing and burning activities in susceptible areas), could considerably improve the extent and quality of habitat available to floricans. Whilst differential habitat requirements between the sexes have been shown (Gray et al., 2009) and should be used to guide any management activities, females were not found to leave the exploded lek areas (Chapter 5) despite their apparent disappearance during the radio telemetry study. However, it is not possible to be sure whether this discrepancy is due to the more complete detection by satellite telemetry of females within the lek areas, or because other grassland habitats to which they were able to move during the radio-tracking study are no longer available, confining females within these last fragments of once much more extensive habitat. Nevertheless, it would seem that BFCAs currently provide appropriate habitats and resources for protecting areas used by both males and females, although females require larger areas than males. These may soon be the only areas of good quality grassland remaining in the floodplain.

The prevention of further losses occurring in areas beyond the BFCAs will be determined by the extent to which the government prevents illegal dam developments, with signs that this is occurring to some degree, although it may be a case of too little, too late (see Chapter 2). Improving land tenure rights of local communities could also help to prevent further large-scale developments (Hirsch, 2011), and ensure that traditional burning and grazing practices continue to maintain the grasslands (Gray et al., 2007). However, external incentives (including access to technology and markets) may also encourage local communities to intensify their use of the floodplain for rice cultivation, so land tenure would by no means preclude the spread of agriculture intensification. Purchase of privately owned rice fields in areas important for floricans is another option which, whilst expensive, may be the only way of securing land. Such areas would require management to restore and then maintain suitable grassland habitat. The rapidity by which grassland reverts following abandonment of deep-water rice fields (Gray, 2008), and the annual flooding which accelerates this process by delivering seeds, rhizome fragments and nutrients, suggest that habitat may develop relatively quickly as long as dams can be removed. However, dam removal would inevitably be expensive.

The effect of disturbance (which is likely to have increased owing to activities associated with dams and rice fields) on nesting floricans has not been studied. Floricans are very wary of people and are likely to abandon nests if disturbance is high (van Zalinge et al., 2009). Whilst the nesting ecology of the Bengal florican has not yet been studied, monitoring of reported

nests would suggest that nest success may be low (van Zalinge et al., 2009). Ways to improve the situation urgently need consideration. To begin with, further research is required to gain a better understanding of nesting outcomes and causes of failure, but a challenge is to achieve this without affecting nest outcomes. Continued work is important within the local communities, to raise awareness and discourage nest disturbance, egg collection and hunting (for the latter, particular effort is required at the onset of the wet season), as well as discussion of the issues surrounding management and timing of ploughing.

Ploughing may have benefits to grassland maintenance (which warrants further investigation) and is necessary for local communities to continue rice cultivation. However, when undertaken in grassland areas in the nesting period (especially with tractors), ploughing must be responsible for destroying a number of nests every year (those that are reported are likely to be a small fraction of the actual number: C. Packman pers. obs.). An agreement is therefore needed on timing, location and methods of ploughing that will minimise threats to nests and maximise benefits to local communities and grassland conservation. Some areas are ploughed simply to mark the land and deter others from claiming it, but are not subsequently cultivated (C. Packman pers. obs.); so if the threat of commercial land-grabbing is reduced, there may be less unnecessary ploughing.

The current system of nest protection, instigated by the Wildlife Conservation Society, involves making payments to people who report nests, with a second payment if the nest is deemed to have succeeded, thereby encouraging them to protect the nests and not to take the eggs. However, there is a risk that this system attracts too much attention and disturbance in the nest vicinity by individuals 'checking on their investment' or merely driven by curiosity, and could increase the likelihood of abandonment.

For another bustard species, the houbara *Chlamydotis undulata*, considerable expertise has been developed in captive breeding techniques (Heezik and Ostrowski, 2001), and could perhaps be applied to Bengal floricans. Whilst this does not tackle the real issue of habitat loss, it may warrant consideration as an 'insurance policy' and to gain time whilst habitat is secured or restored (which could take far longer than the time for the species to go extinct), and could help to bolster population numbers. If eggs were taken only from those nests where failure is certain (e.g. nests discovered whilst ploughing fields or harvesting, when little vegetation remains and the female has not returned, although likelihood of success will diminish the longer the eggs are left), attempts to raise chicks could be trialled, something that has

reportedly already been achieved in Assam from an abandoned egg (Project Bustards, 2011). Whilst this should certainly not be considered in any way an alternative to *in situ* conservation and dealing with the major drivers in the population decline, it may provide a little more security and an additional approach to increasing the population.

Conservation in non-breeding areas

Whilst tagged birds made use of an area of Trea Sameakki BFCA during the non-breeding season, and WCS surveys have also confirmed presence in other parts of this protected area, Tuol Kruel Phan Nheum BFCA has not yet yielded a florican sighting or satellite location. The positioning of these BFCAs was greatly constrained by the authorities, and therefore many higher-use florican areas had to be excluded. Understanding gained of habitat preferences along with mapping of the habitat within the protected areas suggests that Tuol Kruel Phan Nheum contains too much dense forest to be suitable for floricans (Chapter 4). Floricans were found to disperse across large areas of non-breeding habitat (with some remaining in the floodplain grasslands if sufficiently dry). It appears that the population may be much more widely dispersed at this time, with birds from the same breeding sites often using areas quite far apart from each other in the non-breeding season. Targeting multiple small areas of high use, observed from the satellite telemetry data and WCS survey data, may be the only option for creating protected areas now. As a large proportion of used locations were found to be in very open forest, with much evidence of wood harvesting, there is potential to work with communities in managing these areas. The development of plantations is likely to be the greatest threat in the northern areas, with plantations strongly avoided by tagged birds. Land purchases in key pockets of suitable used habitat could, as in the breeding areas, be the only way of ensuring that habitat is not converted.

Tagged florican from the southern breeding sites (Chong Dong and Baray) used areas highly separated from the northern birds and there is currently no provision of protected habitat for the southern population. The stark contrast in habitat availability compared to northern sites, with really only agricultural areas available (which were strongly avoided when all habitat types were present), means more drastic measures may need to be taken in the south to restore an open forest-grassland mosaic in key areas of florican use. Priority areas can be identified from the JICA landcover map (JICA and Ministry of Public Works and Transportation, Cambodia, 2000), which showed that some tagged birds were using localities that had

supported forest in the relatively recent past (i.e. some areas of forest present in 2000, but no longer visible on the 2009 habitat map).

The strong site fidelity shown by adult birds to non-breeding areas suggests they may lack the flexibility to adapt to changing habitat, returning to unsuitable areas when suitable areas are available in the wider landscape (as observed for southern birds). This could also be partly due to conspecific attraction, with birds settling in areas using presence of other floricans, rather than habitat, as a cue (as found for great bustards; Lane and Alonso, 2001). Whilst floricans in the south evidently survive the wet season in agricultural areas, poor quality habitat conditions prior to breeding could have impacts on productivity (Norris et al., 2004; Norris, 2005). It is tempting to speculate that this could even contribute to the lower clutch size of this subspecies relative to Bengal florican in the Indian subcontinent, although this difference is also consistent with the general trend for smaller clutches towards the equator (Cody, 1966; Ricklefs, 1970). Bustards are long-lived (great bustards are estimated to live up to 30 years: (Lane and Alonso, 2001), so there may be a time-lag before the effects on population numbers become evident.

The finding that in dry conditions floricans may remain in the floodplain breeding grasslands throughout the non-breeding season (Chapter 3) is worth considering in relation to potential future changes in flood levels. First, there are concerns (related to fish spawning and migration) that flooding may be affected both by reservoirs built in the floodplain and by the construction of dams on the Mekong river for hydroelectric power, which would restrict the flow of water into the floodplain (Baran and Myschowoda, 2009). If the floodplain experiences lower water levels, more floricans may remain in the grasslands during the wet season. Therefore the importance of the grasslands as non-breeding habitat could increase. Other factors, such as climate change, could also affect future flood depth and extent. A decline in flood extent, however, would reduce soil nutrient replenishment and could lead to changes in grassland composition, cultivation and landuse practices, ultimately to the detriment of the grasslands.

Further research needs

There is still much we do not know about the Bengal florican, including some questions that have important conservation implications. There is little known about the nesting ecology of female floricans, nest outcomes and causes of nest failure. If productivity is currently low, as

suspected, then causes of nest failure clearly need to be identified and ways sought to address them. The use of combined radio and satellite tags deployed on females could considerably improve the likelihood of being able to locate and monitor nests. Nest cameras could be used to assess outcomes and causes of failure, and would also allow interpretation of signs left at nests after hatching, useful for determining the outcomes of nests not belonging to tagged birds. However, use of nest cameras in this environment could be difficult (likelihood of interference with equipment) and potentially increase the risk of abandonment, or of detection by predators, so great care would need to be taken in trialling this method. Combination tags would also allow the tracking of females with chicks and the assessment of their fine-scale habitat requirements. This could be combined with prey (invertebrate) sampling to assess food distribution and how this may change through the seasons. The impacts of disturbance on nest outcomes, such as human activity and grazing in the vicinity of the nest, also need to be examined. However a challenge will be the development of nest monitoring protocols that do not bias the nest outcome.

The potential for habitat restoration should also be explored. An understanding of habitat responses to (e.g.) cultivation frequency, fallow duration, timing of burning, and how this differs between wetter (more fertile) and drier (less fertile) soils and habitats is needed. This would require a long-term study to understand the processes fully.

There is, moreover, the issue of the distribution, abundance and habitat use of the entire population of Bengal floricans in Cambodia. Whilst we have gained knowledge of the birds' movements, sites and habitat use in this study, this has focused on the core population in the south-eastern section of the floodplain (as sites here held an estimated 75% of the population: Gray et al., 2009) and also for logistical reasons. Tagging floricans from other grassland sites identified by Gray et al. (2009, if they remain), both within and beyond the floodplain, would achieve a more comprehensive understanding of wet season movements and non-breeding sites and habitats. Floricans occupying sites beyond the floodplain may be sedentary if flooding is not too extensive. Revisiting all sites surveyed by Gray et al. in 2006/07 would allow rates of grassland loss in other areas of the floodplain to be assessed and florican densities at these sites to be estimated, so that an up-to-date population figure could be obtained and changes in population size determined (this worked is planned for 2012). The methods used in the 2006/07 survey, as well as those currently used to assess the population in the BFCAs, rely on counting displaying males. Examining mating strategies by close observation of male behaviour using radio telemetry could provide useful information as to whether all males display and if

males display not only in their core area but also in outer areas. This would help to determine whether the current monitoring strategy is appropriate, or could be over- or underestimating numbers.

As females are encountered much less frequently, it is difficult to assess their numbers and for total population estimates a 50:50 sex ratio is assumed. However, populations of threatened bird species have a greater propensity for skewed sex ratios (male-biased) and in species with unusual matings systems, such as represented by lekking (female-biased; Donald, 2007). For floricans, either scenario is possible: male-biased sex ratios could result from increased mortality of vulnerable nesting females, whilst female-biased ratios could occur if males are subject to higher predation (by animals or humans) due to their more conspicuous behaviour and colouration (during the breeding season). The accuracy of population estimates could be much improved by factoring in this information. Obtaining accurate estimates of numbers of females is very difficult, however, due to their low detectability, and would require intensive and invasive methods such as rope-dragging across large areas of grassland to flush birds (avoiding the nesting period). Skew in sex ratios can also affect extinction probabilities, with risk lowered in polygynous mating systems when ratios are female- rather than male-biased (Bessa-Gomes et al., 2004), as found for little bustards *Tetrax tetrax* (Morales et al., 2005).

I hope that this thesis has helped to answer some of the unknowns of florican movements and habitat use and that it has assisted in providing some of the evidence needed to develop new and improved conservation strategies for this species. The Bengal florican faces a range of serious threats, and dealing with these is highly complex and challenging. Ultimately an effective solution will require a collaborative effort with strong action from government, local communities and conservation organisations.

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Appendix

Catching Bengal floricans to deploy transmitters

Capture technique

Floricans were captured to enable deployment of backpack-style satellite transmitters. The technique described here is modified from that used by T.N.E. Gray (for deploying radio collar transmitters on Bengal floricans in Cambodia; Gray, 2008), whose method was in turn based on that of T. and L. Osborne (used to catch kori bustards *Ardeotis kori* in Namibia; Osborne and Osborne, 1999).

A 4x4 pick-up truck was used to transport the catching team and equipment and also acted as a mobile hide, allowing floricans to be approached at close range without causing them to fly or hide, as would occur if visibly approached by humans (on foot). A catching team of three was ideal, as once a florican was sighted, one person could remain with the vehicle as a spotter, whilst the other two set up the catching net(s).

On sighting a bird that we wanted to catch, we would first decide on the best location for the net. Most floricans were caught in burned areas, which were either bare or had short grass re-growth. Nets were ideally placed against longer grass at the edge of the burn, to make them less visible and also because floricans are much more easily pushed towards longer vegetation, where they naturally go to hide when they feel threatened. Nets were generally set 50-200m from the bird. Wind direction (if strong) was also taken into account when positioning the net, ideally blowing into the net (rather than sideways or, worst, from behind the net). The terrain and any obstacles for the vehicle (such as wet/soft ground or impassable vegetation) were also considered, as it is necessary to position the vehicle some distance behind the bird, to drive it towards the net.

Once the position of the net was decided, we would drive to the location (taking a circuitous route to avoid disturbing the florican) and position the vehicle between the bird and the net (to help screen net-setting activities). The florican would then be re-sighted (or, if it was hiding, its last location recalled as precisely as possible). A spotter would remain at the vehicle to

watch the location of the bird continuously, if possible standing on the ledge of the doorway opposite the bird and thus partially screened by the vehicle, looking out over the roof (elevation helps keep sight of birds when they hide in long grass). The other two team members would go to position the net. Usually the bird would remain crouched down during the net-setting, but if too close it would fly. Sometimes (especially with females) it would slink away, neck low to the ground.

We used custom-made Ecotone nets (see Table 1 for specifications), supported by wooden poles (approximately 2m high [which helps with locating the net when far away], 3cm diameter). Holes were dug to position the poles in the ground. Two or three poles were used per net. In some instances several nets were deployed simultaneously, forming a continuous line. Nets were often set in a funnel or 'V' shape into which the florican could be pushed. The nets were attached to the poles at approximately 1m above the ground (by looping the top shelf over the pole). The net material was then pulled out loosely behind and laid on the ground, to form a 'tent', into which the florican would be driven.

Once the net was set (this would take 5–10 minutes), the team would return to the vehicle and drive in a wide arc around behind the location of the bird (still watching its location), at a distance of approximately 100m. Usually, after waiting for a short time, this was sufficient distance for the bird to stand up and start walking. The bird was then very slowly approached with the vehicle, at a distance and speed that would encourage it to walk away (towards the net), but not crouch down to hide (or make it fly). If the bird crouched, we would reverse back, until it was relaxed enough to stand up again and continue walking. Gradually the bird would be herded towards the net. The distance at which birds can be herded varies between individuals: some can be approached very close (<10m), others are much more wary and must be herded at a greater distance (>100m). As they approach the net, they often become aware of an obstacle and try to walk around it (it helps to do this at sunset when the net is less visible, or even in the dark when the bird can be herded in the vehicle headlights). At this point quick changes of direction are required whilst driving to keep the bird walking in the required direction into the net, and generally greater pressure was applied once it was close to ensure it would walk into the net. As the bird walks into the 'tent' it contacts the net and may try to walk out backwards or fly up, but usually continuing the approach behind the bird is sufficient to prevent it from backing out and escaping by flying over the net. Once the bird is under the net, flying upwards and flapping causes it to become tangled. It is necessary to watch the bird

closely to ensure it is properly caught, as getting out of the vehicle too soon, before it is fully tangled, may cause it to panic and escape. If the bird ends up on the opposite side of the net (if it flies over for example), it is still possible to drive round and herd it (from the opposite direction) to walk over the net material gathered on the ground, and for it to become tangled, first by the feet and legs, and subsequently by the wings as it flaps.

After fitting with a transmitter, birds were released at >50m from the vehicle, facing away from the vehicle, nets and team members. The bird was placed on the ground and the hood removed just before release. They were released in the open burns, giving them clear passage to run and fly. Releasing them in longer vegetation impeded their movement on departure and made assessing their wellbeing post-release more difficult, as they were more likely to run and crouch in a hidden location, rather than fly. Radio-tagged birds were checked soon after release and again the following day to ensure they were mobile. Satellite-tagged birds could only be checked by examining the first fixes received.

Table 1. Ecotone custom-made net specifications. We trialled different designs but found this to be the best.

Material	Nylon
Mesh size	55x55 mm
Denier	235 (2-ply)
Length	50 m
Height	3 m
Colour	Black
Other	No shelves, topline only (no edge lines), one long loop at ends of topline

Reducing capture myopathy risk

Myopathy, a physiological reaction to stress which can render birds unable to walk and fly, has been reported in a number of captured long-legged species (e.g. Spraker et al., 1987; Nicholson et al., 2000; Rogers et al., 2004), including bustards (Bailey et al., 1996; Marco et al., 2006; Ponjoan et al., 2008). Of the 31 floricans we caught, one (3%) developed myopathy (when handling time was unusually long due to unforeseen external factors), but recovered (left hidden in tall vegetation) after 7 days (when it was able to run and fly). It was sighted later

that season and again the following year. Information on myopathy occurrence gathered from three independent studies of little bustards *Tetrax tetrax* showed 15% of those captured developed myopathy, and nearly half of those subsequently died (Ponjoan et al., 2008). Myopathy is certainly a serious risk factor to consider when catching bustards. After the one case we experienced, we took extra precautions to reduce the risk of myopathy occurring, by keeping handling time as short as possible (<20 minutes, as recommended by Ponjoan et al., 2008) and ensuring noise and movement around the bird were minimal. We had no further cases of myopathy and the tracking data showed all tagged birds survived >6 months post-capture, ruling out any capture-related mortality.

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