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Tracking sarus crane movements in Cambodia and Vietnam reveals seasonal vulnerabilities and gaps in protected area coverage

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ABSTRACT: The movements of 17 eastern sarus cranes *Grus antigone sharpii* in Cambodia and Vietnam were tracked during both wet and dry seasons in 1998–2002 and 2015–2017, revealing previously unknown but important sites. Crane breeding territories were located in Cambodia's northern dry deciduous dipterocarp forests, with territories of cranes captured in the Tonle Sap basin located further west and more likely to fall within protected areas than those captured in the Mekong Delta. During the non-breeding (dry) season, cranes returned to sites in which they had originally been captured. Most cranes initially used a different part of the same floodplain in the early stages of the dry season, but cranes from the Mekong Delta that nested west of the Mekong River would initially stop in the eastern Tonle Sap floodplains before continuing to the Mekong Delta floodplains. Protected area coverage of key dry season habitat within the Tonle Sap basin was lower than in the Mekong Delta. Out of 5 juveniles tracked in 2015/2016, 1 disappeared, 1 died and 1 was injured; 1 adult also disappeared. All mortality and disappearances occurred during the wet season and at least 1 mo after capture. Persistence of the eastern sarus crane will require improvement of protected area coverage of both breeding areas and previously unknown but important sites used during the dry season. In the dry season, engagement of farmers in conservation efforts is also important, as crane home ranges included agricultural areas even in the direct surroundings of protected wetland habitat.

KEY WORDS: *Grus antigone* · Satellite tracking · Migration · Home range · Conservation · Mortality · Nesting

1. INTRODUCTION

Flight allows birds to utilize non-contiguous habitats, and many species migrate as a learned response to seasonal patterns in the availability of resources (especially food) in different regions (Newton 2004). However, migratory birds are inherently vulnerable because they depend on food and safety at multiple sites, with any one site potentially compromising the conservation of otherwise secure species (Runge et al. 2015). Successful conservation of migratory species may be contingent on using annual movement patterns to identify sites where conservation actions may be required (Yong et al. 2022). Tracking of migratory birds is increasingly providing details on previously unknown linkages between breeding and non-breeding areas (Chen et al. 2021, Xi et al. 2021), differences in the use of areas between subpopulations (Deng et al. 2021) as well as seasonal habitat preferences and movement choices (Traill et al. 2010, Chen et al. 2021). New, important use areas have been identified, suggesting the need for the place-

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ment or modification of conservation areas (Montevecchi et al. 2012, Xi et al. 2021) or reintroduction sites (Van Schmidt et al. 2014). Intensive monitoring of individuals has also helped us better understand the risks to which migrating birds are exposed (Montevecchi et al. 2012, Santos et al. 2021) and aided in the calculation of survival rates (Rotics et al. 2021).

In the USA, tracking species' movements has been integral to a major conservation effort that halted the decline towards extinction of the largely migratory whooping crane *Grus americana* (Cannon 1996, Pearse et al. 2020). Other migratory crane species, such as the Eurasian crane *Grus grus*, have also been the subject of successful collaborative conservation interventions once their migratory paths were known (Prange 2005). Such information is needed to help understand what regulates the population size (Bridge et al. 2011) of the eastern sarus crane in Cambodia and Vietnam and what is needed for effective conservation of the population.

Previous knowledge of sarus crane distribution and movements in Cambodia and Vietnam comes from early survey work carried out by multiple governmental agencies and non-governmental organizations from the late 1980s onwards in Vietnam and from the early 2000s in Cambodia (Seng et al. 2003, Buckton & Safford 2004). These surveys identified Important Bird Areas (IBAs), many of which became protected areas between 2001 and 2011. Included among these regions were 3 sarus crane conservation areas in Cambodia that together encompass some of the most important remaining dry season habitats.

Surveys of the cranes during the dry season have highlighted gaps in our understanding of the movements and distribution of the population. This includes a lack of information on where cranes from the monitored dry season protected areas move to in the wet season, dispersal behaviour of juveniles after independence, selection of habitats within the different seasons and how comprehensively the current protected area system covers important crane habitat during the entire annual cycle. Here, we present some answers to these questions derived from tracking the movements of sarus cranes in Cambodia and Vietnam in 1998–2002 and 2015–2017.

2. MATERIALS AND METHODS

2.1. Study sites

The climate within the range of sarus cranes in Cambodia and Vietnam is dominated by monsoons. Winds blowing from the southwest bring heavy rainfall from mid-May to early October, at which time the Mekong River, with an average annual total discharge volume of 475 km^3 (Vastila et al. 2010), floods vast areas of the Tonle Sap Lake and Mekong Delta in Cambodia and Vietnam. Flood pulses in the Mekong River are sufficient to reverse the flow direction of the Tonle Sap River, causing Tonle Sap Lake to expand to 15 000 km^2 (Campbell et al. 2006). There is then almost no rain from early November to mid-March (Thoeun 2015), and Tonle Sap Lake shrinks to as little as one-sixth of its monsoonal area (van Zalinge et al. 2004).

Sarus cranes in this region have adapted to periods of flood and drought by making seasonal movements between breeding and non-breeding areas. In the dry season, they use 2 distinct regions: the northern part of the Tonle Sap floodplain, including the Ang Trapeang Thmor reservoir, and various sites in the Mekong Delta of Vietnam and Cambodia (Fig. 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/n050p151_supp.pdf). At the onset of monsoonal rains, adult cranes migrate from these floodplains to open deciduous dipterocarp forest with scattered small wetlands (van Zalinge et al. 2023). These areas are almost exclusively within northern Cambodia (van Zalinge et al. 2023), with only one confirmed record from such open forests in Vietnam over the last 30 yr (Nguyen 2004).

Capture sites were located in the dry (non-breeding) season in areas known to hold large aggregations of cranes or where crane presence was otherwise predictable: Ang Trapeang Thmor Sarus Crane Conservation Area, Anlung Pring Sarus Crane Conservation Area, Stoung-Chikraeng Bengal Florican Conservation Area and Tram Chim National Park.

This study combines data from cranes captured in 3 different years:

(1) 1998: 4 family groups (pairs or pairs with chicks) were captured. Of these, 4 adult birds received satellite transmitters (2 males and 2 females) but only 3 were independent, as 2 adults receiving transmitters were paired with each other. Additionally, 1 female and 2 juveniles were colour-banded only. Capture occurred during the dry season at Tram Chim National Park, within the Mekong Delta of Vietnam.

(2) 2001: 1 family group was captured, and the female as well as both accompanying juveniles received satellite transmitters. The male was colour-banded only. Capture occurred at Tram Chim National Park.

(3) 2015: 5 family groups were captured and received satellite transmitters (1 male and 1 juvenile

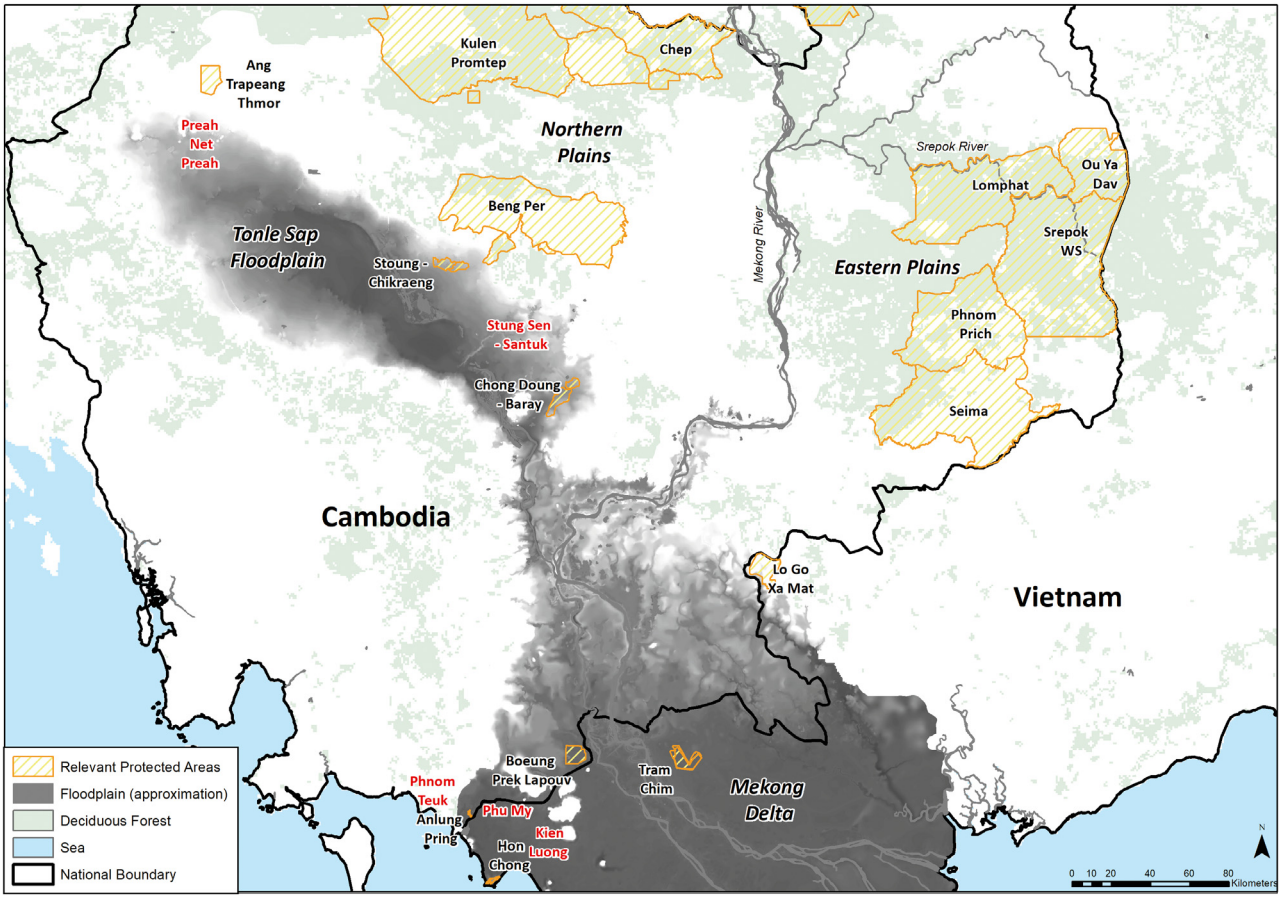

Fig. 1. Relevant protected areas and other important areas (names in red) used by sarus cranes in the northern part of the Tonle Sap floodplain, including the Ang Trapeang Thmor reservoir and various sites in the Mekong Delta of Vietnam and Cambodia

per family). Four females and 2 juveniles were colour-banded only. Two family groups were caught in Anlung Pring Sarus Crane Conservation Area within the Mekong Delta of Cambodia. Three other crane families were caught in the Tonle Sap floodplain region: 1 in Ang Trapeang Thmor Sarus Crane Conservation Area and the other 2 in the Stoung Bengal Florican Conservation Area.

2.2. Deployment of transmitters

In March 1998 and March 2001, we deployed a total of 7 battery-powered ARGOS satellite Platform Transmitter Terminal (PTTs) manufactured by Microwave Telemetry (www.microwavetelemetry.com). In January–February 2015, 10 solar-powered General Packet Radio Service–Global System for Mobile Communications (GPRS–GSM) transmitters were deployed. These devices were manufactured by e-obs (www.e-obs.de). Hereafter, all tracking devices are referred to as 'tags'.

In all 3 study years, cranes were captured by tranquilizing them using alpha-chloralose applied to bait (Hartup et al. 2014). This capture technique has the lowest morbidity rate for any known capture technique of cranes and has been used by the International Crane Foundation since 1990 (Hayes et al. 2003). The use of alpha-chloralose reduces the risk of injury during capture and lowers stress levels during handling compared to methods that require the physical restraint of non-sedated birds (Hayes et al. 2003, Hartup et al. 2014). Importantly, use of alpha-chloralose allows entire family groups to be caught, which provides greater power in interpreting ecological data obtained from different age groups (Hayes et al. 2003, Wheeler et al. 2019). To reduce problems with exertional myopathy, a common side-effect of capturing cranes (Hartup et al. 2014), birds captured in 2001 received at least 100 ml of the anti-inflam-

matory carprofen with lactated Ringer's solution delivered subcutaneously during processing as well as a vitamin E–selenium mixture administered intermuscularly (right breast) after processing, to aid recovery from the effects of alpha-chloralose. In 2015, only lactated Ringer's solution was given, but more fluid (200–250 ml) was provided per individual.

All tags were attached with backpack harnesses following Nagendran et al. (1994). This method involved using a single Teflon ribbon looped through transmitter holes and over the wings, with the ribbon crossing at the breast, forming a figure-8 pattern. Ribbon ends were stitched with a degradable thread and designed to unravel completely once broken, allowing the tag to fall off quickly with a single break in the harness. Each individual that was caught received a combination of 2 coloured bands on each leg and a single metal band with contact details inscribed. All bands were placed above the tibiotarsal joint (Dickerson & Hayes 2014). All harnesses, colour bands and tags used had a combined weight of <150 g bird^{-1}, which was 3% of the smallest individual captured (4900 g) and within the recommended 2–3% range of total body weight (Sutherland et al. 2004). For each individual, gender (based on relative size of adults and vocalizations made during the capture) and age (adult: bare, red-skinned heads; 1st year/juvenile: brown feathered heads) were recorded.

Birds were kept in a holding pen for recovery after processing. Individuals were checked for release approximately 1 h before sunset and were released if all members of the family unit were alert and active. If at least one bird was still sedated, all birds were kept overnight. The condition of the birds was then checked again in the morning, and they were released simultaneously if all had recovered. No captured birds showed signs of exertional myopathy, and no crane was released later than the morning after capture. After releasing each family group, birds were observed for 2–3 d to evaluate their condition and behaviour. No birds exhibited post-release behavioral problems, and family groups remained intact.

2.3. Data collection and analysis

For GPRS–GSM tags, coordinate data recorded by the GPS were transmitted daily by either GPRS (wireless internet; if good connection speeds were available) or by SMS (if GPRS transmission was not possible). If neither system was available, data were queued for later transmission. Where long periods without GPRS capability occurred, cranes were located from the ground and data downloaded through a hand-held radio receiver. When solar panels did not work effectively (presumably because feathers were preened over the solar panels), battery power quickly diminished. In response, functions turned off until the required charge levels became available again. PTTs were programmed to record and transmit 1 coordinate per day, allowing for 1 yr of data collection before the battery expired. Whether a point was recorded depended on the ability of the transmitter to establish satellite links. With the GPRS–GSM tags, but not the PTTs, it was possible to communicate with the tags to change settings after deployment. This proved necessary, as solar charging was variable which, in turn, influenced how frequently data could be collected. Daily charging of the tags varied by crane age, with adults typically preening their feathers over the tag more frequently, but this behaviour also varied by individual. Although initially a GPS location was obtained every 5 min, eventually a setting of 1 GPS location per day was chosen, as had occurred with the PTTs. However, the rate at which we scaled back to a single location per day varied by individual. After recording a location, the tag would attempt to transmit the location via GPRS or GSM. The success of these daily cycles depended on whether enough electrical charge had been generated since the previous attempt, although weather and remoteness also influenced the possibility of establishing a link. Unsent data was stored, and sending was re-attempted in subsequent cycles.

Combining data from all tracking periods, we used Zoa Track (www.zoatrack.org), an online tracking data repository, to calculate 50% (core) and 95% minimum convex polygon (MCP) home ranges with each individual/season/year as an independent sample. This approach uses the smallest area convex set that contains the location data (Worton 1995). The calculations were performed within R in ZoaTrack using the 'adehabitatHR' package (Calenge 2006). Potential pseudo-replication was tested for in a generalized linear mixed model of individual home range sizes against season and year as fixed factors and with individual as a random effect. There was no improvement in model performance (Akaike's information criterion adjusted for small sample sizes; $\Delta AIC_c = 4.2$) over the base model without individuals as random effects; therefore, it was permissible to use home range measurements from the same individual for different years. Before using PTT data in

our analysis, we removed all points with locational errors of >1.5 km, as per the Argos locational error categories. Data from the GPS tags were also checked for obvious locational errors.

Though 10 adults were tagged, 2 adults were members of the same pair and were expected to travel together, so we had independent samples of movement from 9 adults. One tag on an adult failed within 1 mo and provided too few data points for home range analysis, making a total of 8 adults providing independent samples. A total of 7 juveniles were tagged: 2 in 2001 and 5 in 2015. The 2 juveniles captured in 2001 were siblings, remaining close together and following their parent in both the dry season of capture and the subsequent wet season. Only in the following dry season, in their second year of life (i.e. as sub-adults) did they occupy different areas. Because they did not represent independent samples, in subsequent analysis their home range values were averaged, giving 6 independent values. Movement and home range data of a juvenile that was recaptured and then necessarily released into the only available flock of non-breeding cranes in Varin — which is part of the region used by the Tonle Sap subpopulation, instead of the Mekong Delta where it was originally captured — were not used after the 2015 wet season re-release. The data from a previously untagged juvenile confiscated in the Tonle Sap floodplains and later released with a tag in Varin, along with the previous juvenile, were not used in the analysis of the period directly following release but were used for the home range analysis of sub-adults in 2017.

We compared the mortality rate of tagged cranes between 1998–2001 and 2015 for the 2 yr period after initial capture. To improve estimates of mortality rates, we searched for banded individuals after tags expired. For 1998 and 2001, any resighting up to the 2017 dry season (March) was recorded. From 2016–2017, the study team searched intensively for banded cranes at the capture sites (Ang Trapeang Thmor, Anlung Pring and Stoung) on a monthly basis during the dry season. Resighting data provided by observers other than the study team were also used when accompanied by photographs of sufficient quality to identify band combinations. Birds in juvenile plumage had hatched during the wet season preceding capture, e.g. juveniles caught in January or February 2015 would have hatched in the 2014 wet season, most likely between June and September, approximately 6 mo earlier. For juveniles captured in 1998 or 2001, we provide an estimate of the average age reached based on the last year of resighting between 1998–2001 and 2017 as well as the annual resighting probability for all cranes in that period, calculated as the percentage of number of years with resightings from first to last resighting as a fraction of the total number of years in the same period. Sarus cranes in captivity have first been recorded breeding when 5 yr old (Johnsgard 1983).

We used ArcGIS v.10 (www.esri.com) for mapping purposes and analysis of protected area overlap with crane home ranges.

3. RESULTS

3.1. Movement patterns

A total of 222 location points, with a minimum accuracy of 1.5 km, were obtained from PTTs from 11 March 1998 to 21 March 1999, and a further 307 points were obtained from 5 March 2001 to 4 April 2003. Data were obtained from 3 adult females, 2 adult males and 2 juveniles belonging to 4 different family units that had been captured in the Mekong Delta at Tram Chim in the dry season (see Table S2). From 4 February 2015 to 26 June 2015, a total of 23 321 GPS points were obtained from an adult male and 2 juveniles from 2 different family groups captured in the Mekong Delta at Anlung Pring during the dry season. From 29 January 2015 to 7 June 2017, a total of 24 551 GPS points were obtained from 3 adult males and 3 juveniles from 3 family units captured in the Tonle Sap floodplains (Stoung and Ang Trapeang Thmor) during the dry season, plus the additional bird released after confiscation.

3.1.1. Mekong Delta

Post-capture, cranes remained at their capture site or utilized sites nearby. In the remainder of the 2015 dry season, cranes captured in Anlung Pring (Cambodia) also used Phnom Teuk (Cambodia; 5 km west of Anlung Pring), Phu My (6 km east of Anlung Pring in Vietnam) and Kien Luong (24 km east of Anlung Pring in Vietnam; Fig. 2). Daily movements occurred between Anlung Pring, where most cranes roosted and often fed, and the additional foraging areas in Phnom Teuk or Phu My. One of the tracked families chose to roost by themselves at Phu My post-capture. When using Kien Luong, cranes would feed during the day and roost at night in that vicinity. No tracking data were obtained during the following dry season for cranes captured and tracked in the delta during

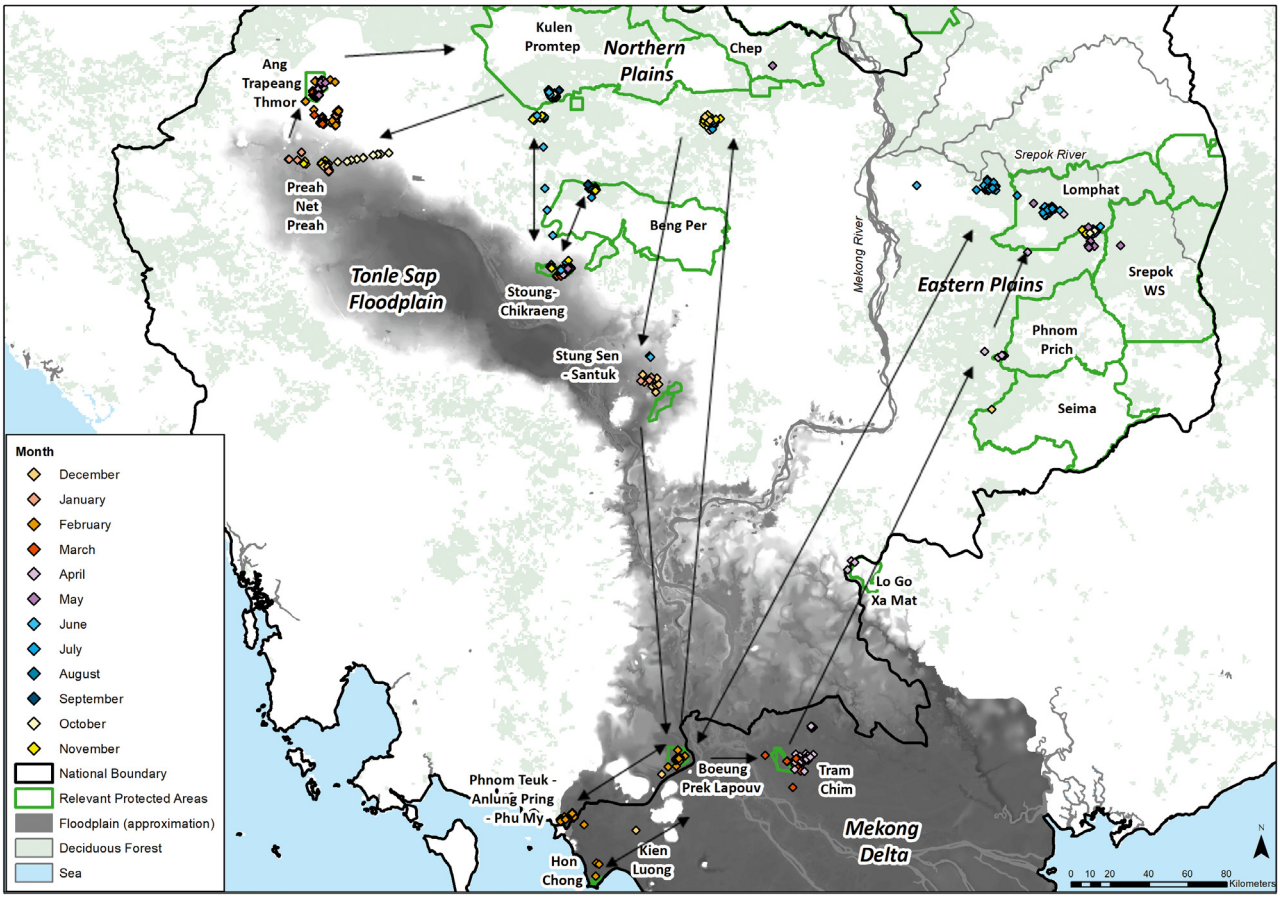

Fig. 2. Monthly locations (coloured symbols) of adult sarus cranes and their general movement patterns (arrows)

2015. However, 3 out of 4 adult birds were resighted at Anlung Pring in January 2016, as was a single bonded pair in March 2017.

Cranes captured at Tram Chim (Vietnam) in 1998 and 2001 roosted and fed primarily at Tram Chim from capture in March until leaving the delta for wet season sites in mid-April. The family group captured in 2001, however, stopped briefly at another Mekong Delta site in Vietnam (Lang Sen Provincial Park; 10 km ENE of Tram Chim), before leaving the delta and continuing on to wet season sites. The average (±SE) departure date for adults was 16 April ± 1.6 d (n = 5). On returning to the Mekong Delta in the following dry season, 2 adults used Boeung Prek Lapouv (Cambodia): one from 26 January to 7 February 1999; the other from 31 December 2001 to 28 February 2002, before moving on to Hon Chong (Vietnam) and Tram Chim, respectively, where transmission ended.

One of the 2 adults, coming from its wet season territory southeast of Kulen Promtep Wildlife Sanctuary, first used an area in the southeastern corner of the Tonle Sap floodplain (Stung Sen–Santuk) from around 5 December 1998 to at least 15 January 1999 before continuing to the Mekong Delta (Boeung Prek Lapouv and Hon Chong). The same area was used by a juvenile from the Mekong Delta in 2015 at the start of the wet season.

One of 2 juveniles (then a sub-adult) used Hon Chong from 3 January to at least 2 February 2002 before transmissions ended. The other juvenile did not transmit data in 2002. Their parent, based on a single record in the vicinity and dates of earlier and later points, is also likely to have visited Hon Chong before moving to Boeung Prek Lapouv and Tram Chim.

Two out of 3 adult cranes from independent family units tagged in 1998 and the adult female tagged in 2001, along with her chicks, moved northwards in April to locations southeast of Lomphat Wildlife Sanctuary in the Eastern Plains (Cambodia) and stayed there during the wet season. The family group stopped at Lo Go Xa Mat National Park (Vietnam), which is outside the Mekong Delta and approximately 100 km from Tram Chim, on 14 April before

arriving at a location about 10 km northwest of their wet season territory on 18 April. The tagged birds then moved south to a site near Phnom Prich Wildlife Sanctuary (about 50 km NE of Kratie) for a minimum of 7 d (24–30 April) before returning to their territory used for the rest of the wet season on 2 May. The remaining adult from 1998 also moved north in April but to a location southeast of Kulen Promtep Wildlife Sanctuary in the Northern Plains, west of the Mekong River (Fig. 2). The arrival at potential nesting areas was no later than 28 April and no more than 8 d after departing Tram Chim. Unlike the other birds captured in 1998, no stopping locations were identified between the Mekong Delta and Chep. Distances travelled by tagged cranes between dry and wet season sites were 307, 310, 312 and 332 km (x = 315 km).

Data received from 3 other transmitters in 1998–1999 (but only 2 independent adults as 2 individuals were a pair) indicated that the birds, or at least the tags (if they fell off), were still in the wet season areas on 17 February, 21 March and 25 March, well into the dry season. All these dates were also the last transmissions of the tags.

The arrival of adults on what were likely breeding territories occurred between 28 April and 11 May in 1998 and 2 May in 2001. In 2015, only a single record from 1 adult was received in the wet season on 26 May, in the Chep Wildlife Sanctuary. The bird probably nested in that general area, as it returned to Anlung Pring with 1 chick in the 2016 dry season. No further data were received from tags of adults tracked from the Mekong Delta in 2015.

The movement patterns of tracked juveniles (Fig. 3) showed marked differences between 2001 and 2015 at the start of the wet season. Two juveniles from 2001, belonging to the same family unit, moved north together with, and remained in the same area as, their tracked parent throughout the wet season. In 2015, even though all juveniles ranged widely, the movements of 2 tagged juveniles from the Mekong Delta were particularly extensive. One juvenile flew

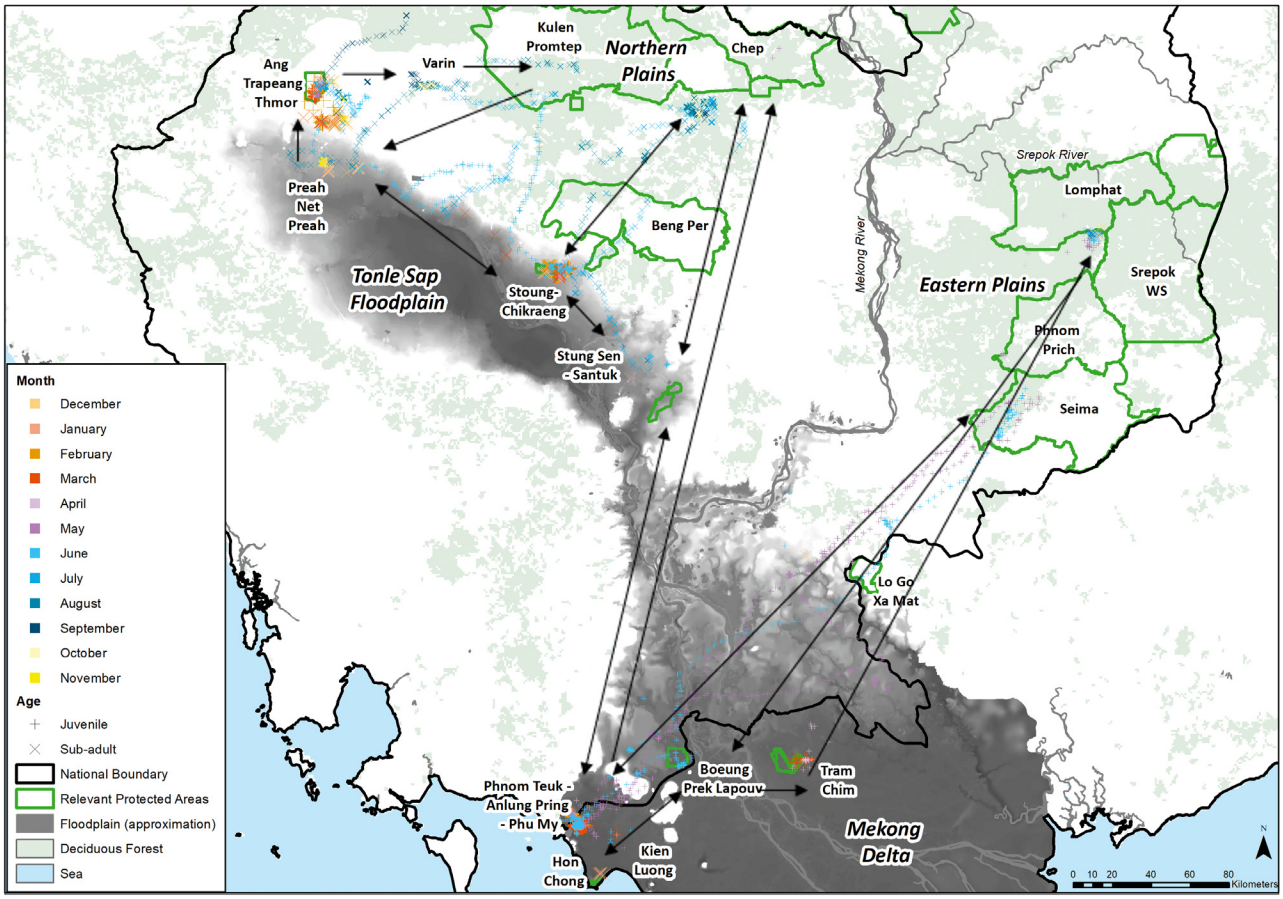

Fig. 3. Monthly juvenile (approx. 0.5–1.5 yr) and subadult (approx. 1.5–3 yr) locations (sizes of + and × symbols vary for better visibility)and their movement patterns (arrows)

from Anlung Pring to the probable breeding area of its parents in Chep on 3 May, visited Chep and Santuk in the Tonle Sap floodplains on 19 May and again from 29 May to 8 June and then returned to Anlung Pring on 12 June, travelling a total distance of over 1200 km in 2 mo. The other juvenile flew twice from Anlung Pring to the Eastern Plains, a total of just under 1000 km in less than 2 mo.

3.1.2. Tonle Sap floodplain cranes

All cranes remained at the sites where they had been captured until the end of the dry season, except for a short move by one of the families from Stoung to Santuk from 5–10 June (adult) and 5–13 June (juvenile). Tagged adults then travelled 47, 80 and 120 km ($\bar{x}$ = 82 km) to likely breeding territories on the Northern Plains (breeding was confirmed for the adult male from Ang Trapeang Thmor; a nest with a single egg was found on 19 August and signs of recent hatching on 27 August). The last 2015 record from the adult at Ang Trapeang Thmor was 18 April (Table 1), while the 2 adults at Stoung remained until 18 June and 16 July, the latter having moved briefly to its wet season site around 27 June but then returned to Stoung. Juveniles stayed longer than their parents. The juvenile from Ang Trapeang Thmor remained there until 29 May, one juvenile from Stoung remained until 10 July and the other until early August before moving within the floodplain to near Santuk, where it was captured for the wildlife trade. From 11 July to 27 October 2015, the remaining juvenile from Stoung used a location 16 km southeast of Tbeng Meanchey, the capital of Preah Vihear province, while in subsequent years as a sub-adult, it used a location 13 km northwest of Tbeng Meanchey (from 28 May–27 December in 2016 and from 16 April until last transmission on 7 June in 2017; see locations and seasonal movement patterns of all juveniles in Fig. 3). The juvenile from Ang Trapeang Thmor moved frequently, occasionally visiting Ang Trapeang Thmor and the Tonle Sap floodplain but mostly using flooded agricultural fields near Varin village (Fig. 3). At this time, it was in a group with 6 other juveniles. It also made substantial movements in the 2016 wet season as a sub-adult, but spent 3 August to 19 November 5 km west of Prey Veng village within Kulen Promtep Wildlife Sanctuary.

Table 1. Site use by tagged sarus cranes returning to Tonle Sap floodplains in their second and third years

Individual (tag number)	Age group	Capture site	Date of return	Site of return	Last record at site of return	Destination
2016 Dry season						
14233	Adult	Stoung	5 Nov 2015	Stoung	10 May 2016	Wet season site
4237	Sub-adult	Stoung	28 Nov 2015	Stoung	27 May 2016	Wet season site
4239	Adult	Ang Trapeang Thmor	29 Oct 2015	Preah Net Preah	25 Jan 2016	Ang Trapeang Thmor
			25 Jan 2016	Ang Trapeang Thmor	24 May 2016	Wet season site
4240	Sub-adult	Ang Trapeang Thmor	23 Oct 2015	Preah Net Preah	6 Jan 2016	Ang Trapeang Thmor
			6 Jan 2016	Ang Trapeang Thmor	9 Jun 2016	Wet season site
2017 Dry season						
4237	Sub-adult	Stoung	29 Dec 2016	Preah Net Preah	18 Jan 2017	Ang Trapeang Thmor
			18 Jan 2017	Ang Trapeang Thmor	30 Mar 2017	End transmission
4240	Sub-adult	Ang Trapeang Thmor	21 Nov 2016	Preah Net Preah	16 Jan 2017	Ang Trapeang Thmor
			16 Jan 2016	Ang Trapeang Thmor	18 Apr 2017	End transmission

Cranes returned to the Tonle Sap floodplain from late October to late December (Table 1). Birds captured at Ang Trapeang Thmor tended to return there via Preah Net Preah, where they stayed until January. One adult and 1 juvenile captured at Stoung returned there, although 1 sub-adult also travelled to Ang Trapeang Thmor via Preah Net Preah in 2017.

3.2. Home range size

3.2.1. Dry season

From capture to departure for wet season habitats, average core home ranges of adults were smaller than those of juveniles (Table S3; $\bar{x}$ ± SE: adults: 3.3 ±1.8 km^2, n = 8; juveniles: 6.2 ± 2.3 km^2, n = 6), suggesting that juveniles disassociated from adults while using dry season habitats. Crane home ranges between the Tonle Sap floodplains and the Mekong Delta were of similar size (Tonle Sap: 4.9 ± 2.4 km^2, n = 6; Mekong Delta: 4.3 ± 1.9 km^2, n = 8) in the first dry season, with tracking only starting in the late dry season (end of January–early March); however, when combining all dry season movement data, the average of core home ranges in the Tonle Sap (42.7 ± 18.1 km^2, n = 11) was substantially larger than that within the Mekong Delta (3.7 ± 1.6 km^2, n = 10). Cranes using Ang Trapeang Thmor in the dry season had especially large home ranges.

3.2.2. Wet season

Seven independent adults (3 from the Tonle Sap floodplains captured in 2015 and 4 captured from the Mekong Delta in 1998–2001) had an average core home range (50% MCP) of 6.6 ± 3.8 km^2 (Table S3).

Of 3 juveniles tracked for the entire wet season, the average core home range was 140.3 ± 82.03 km^2, but this figure is much larger if the long-distance movements of 3 other juveniles to and from wet and dry season sites at the start of the wet season are included (average 50% MCP: 1857.4 ± 1378.9 km^2). The latter 3 juveniles were subsequently captured by people, or transmission ended abruptly through unknown cause, in the first months of the wet season (see Section 3.4).

The average core home range of juveniles, then sub-adults, tracked over a second wet season (including a bird confiscated and released in the Tonle Sap region in 2015) was 94.2 ± 82.3 km^2 (n = 3). Juveniles from 2001 overlapped their wet season habitat use with their parents substantially, whereas the juvenile/subadult from Stoung occupied distinctly different wet season locations from its parents' wet season territory in both 2015 and 2016 (55 and 60 km away, respectively). The juvenile/subadult from Ang Trapeang Thmor used a very different area in 2015, about 70 km from its parents' territory, but had a core home range that slightly overlapped that of its parents in 2016.

3.3. Protected area coverage

3.3.1. Dry season

The average protected area coverage for all adult core home ranges in the dry season in all regions and years was 64.7% (n = 11; Table S4); 73.5% (n = 7) in the Mekong Delta alone and 49.4% in the Tonle Sap floodplains (n = 4). Cranes in the Tonle Sap region tended to use floodplains with no official protected status early in the dry season, and cranes using Ang Trapeang Thmor often foraged in unprotected rice fields surrounding the reserve (Fig. 2).

Since juveniles became independent late in their first dry season, overlap with protected areas resembled that of adults. In 2016 and 2017, 25.7% of the core home ranges of 2 sub-adults from the Tonle Sap region overlapped with protected areas. As with adults, use of unprotected habitats centered on Preah Net Preah and rice fields outside of Ang Trapeang Thmor.

3.3.2. Wet season

Of the 7 adults tracked sufficiently well to allow estimates of wet season home range, 3 had home ranges entirely within protected areas, 3 entirely outside and one with a 6% overlap (Fig. 4, Table S5). First-year juveniles only had an 8.8% overlap with protected areas (Table S5). The two 2001 juveniles that had spent their first wet season close to their parents' territory on the boundary of Lomphat Wildlife Sanctuary remained entirely outside the protected area but still within natural habitat. For the 3 Tonle Sap individuals for which data were available in the second year, the overlap of core ranges with protected areas increased to 61.4%.

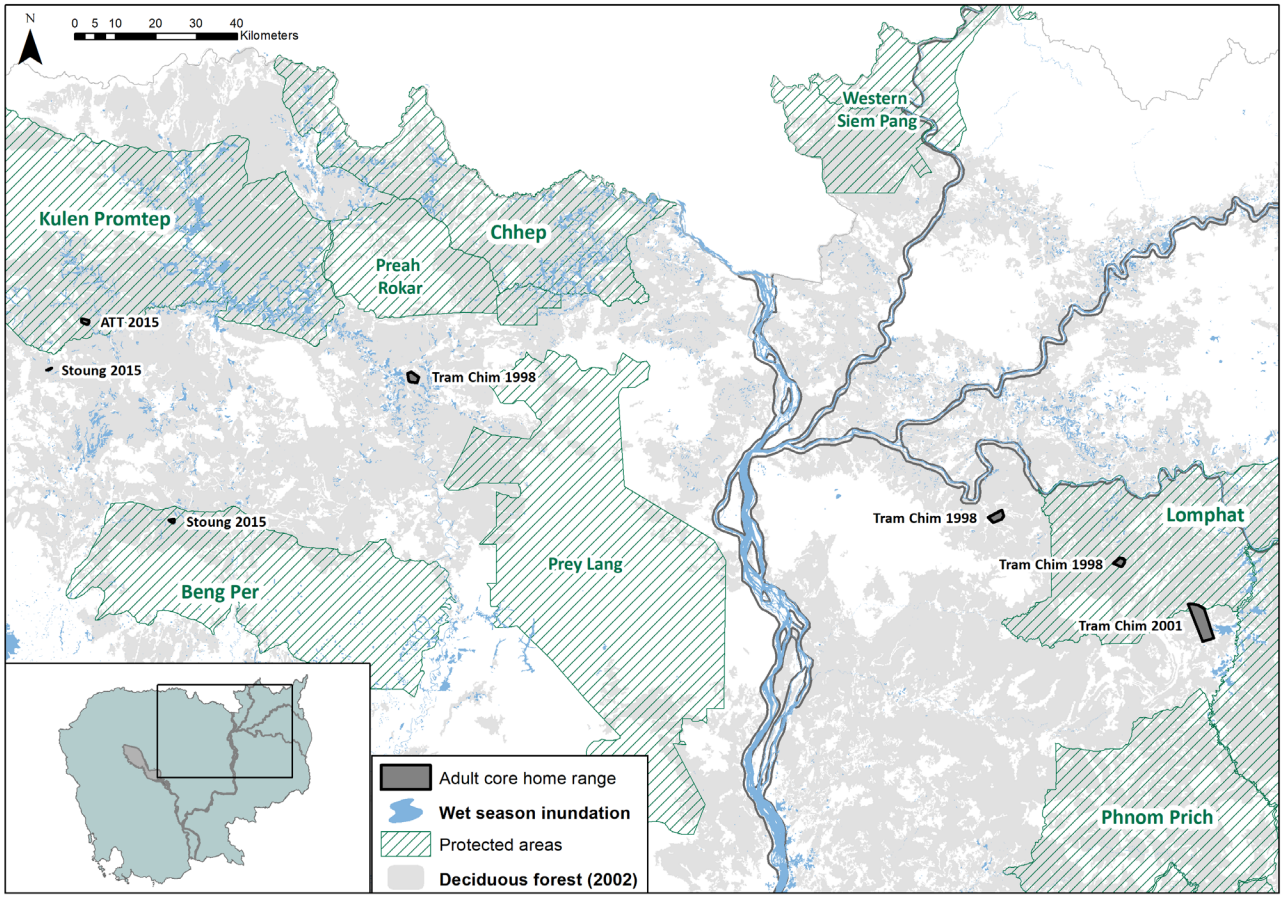

Fig. 4. Adult sarus crane core home ranges in the wet season. ATT: Ang Trapeang Thmor

3.4. Mortality

Of the 5 adults tagged in 2015, one (20%) did not return to its dry season capture site in either 2016 or 2017, although its partner was seen, alone, in 2016 (Table S6). One in 5 (20%) tagged adults from 1998 and 2001 were not resighted beyond 2 yr after capture. This is 1 in 4 (25%) for completely independent adults, as 2 were a bonded pair. Three of 5 juveniles tagged in 2015 did not return to capture sites in the following dry season (2016). Two tracked juveniles were captured by people soon after they became independent of their parents. One juvenile from the Mekong Delta was said by police to have been too weak to fly when caught in rice fields by local people on 25 June 2015. A second juvenile from the Tonle Sap floodplains was trapped for the wildlife trade on 5 August 2015 along with another unknown juvenile. Transmissions from a third juvenile ended suddenly on 25 June 2015 in Seima Wildlife Sanctuary, but no remains were found when the area was visited 5 d later. It was not resighted in 2016 or 2017. The single juvenile tagged in 2001 was resighted in 2015, becoming the crane with the longest series of resighting data and at that time having reached an age of 15.5 yr. On average, juveniles banded in 1998 or 2001 were resighted up to 6.3 yr (n = 4) after capture, corresponding to an average age of 7.8 yr, although this is likely an underestimate as the annual resighting probability was 53.4%.

In 2017, 2 yr after capture, 2 of 4 adults resighted had lost their transmitters, while the 2 remaining juveniles still had theirs. For a 2 yr period following initial capture, average survivorship — based on resighting data from 1998–2017 (Table S6) of cranes captured in 1998 and 2001 that were both banded and fitted with transmitters (71.4%; n = 7) — was similar to that of cranes that were banded only (75%; n = 4).

Of the 4 adult pairs resighted in 2016, one from Anlung Pring had a single offspring with it. The adult from Ang Trapeang Thmor that was known to have nested did not have young when it was resighted at Ang Trapeang Thmor in 2016. When located, the nest site had recently been disturbed by dogs.

4. DISCUSSION

4.1. Dry season distribution

4.1.1. Tonle Sap floodplains

In the Tonle Sap floodplains, the presence of non-breeding flocks of sarus crane in the dry season was already known for Ang Trapeang Thmor northwest of the Tonle Sap floodplain and Stoung in the central floodplain, but tracking revealed an unsuspected staging post at Preah Net Preah in the northwestern corner of the Tonle Sap floodplain that was repeatedly used by cranes for foraging in the early dry season. Cranes foraged at Preah Net Preah for several months in the early dry season before moving to Ang Trapeang Thmor, with food being less available to cranes in herbaceous floodplains as they dry (Meynell et al. 2012, Yav et al. 2015). At the Ang Trapeang Thmor reservoir, water levels generally receded more slowly, even though water levels were not managed in consideration of cranes, making food in the *Eleocharis dulcis* wetland more accessible later in the dry season. While Preah Net Preah was already listed as an IBA (Seng et al. 2003), its importance for cranes had not been documented, nor had a link with Ang Trapeang Thmor been established. Once at Ang Trapeang Thmor, the tagged cranes that moved to Ang Trapeang Thmor in December–January also foraged extensively in rice fields near the reservoir since the wet season crop had been harvested by December, making waste grains available. These flocks consisted of loose aggregations of all social groups: families, paired adults without young, unpaired adults and immature birds.

In contrast to these larger flocks at Ang Trapeang Thmor, only a few individual family groups used the floodplain site on a continuous basis throughout the dry season at Stoung. There, suitable habitat, consisting of a few smaller permanent ponds scattered within a mosaic of grassland and rice fields, was used throughout the dry season. Tracking also established a connection between Stoung and other sites. In the first year, all adults and the 4 juveniles that were still alive returned to Stoung; however, during the following year, 3 juveniles captured at Stoung were present at the Preah Net Preah and Ang Trapeang Thmor sites. The small water sources at Stoung were apparently sufficient for the small family groups that used them and the surrounding grassland–agricultural mosaic, even throughout the exceptionally long dry season of 2015. In that year, an adult moved from Stoung to the forests 45 km to the north in June only to return immediately, departing again 1 mo later to establish a breeding territory for the remainder of the wet season. Similar climate-driven adjustments to migration have been seen in temperate-breeding sandhill cranes *Grus canadensis*, where adults that had returned to breeding areas early were forced to return to staging areas for several weeks when the weather turned exceptionally cold, travelling approximately 200 km (Thompson & Lacy 2016).

4.1.2. Mekong Delta

Tagged cranes linked to the Northern Plains stopped at a previously unknown site in the southeastern corner of the Tonle Sap floodplain, near Santuk. A single adult stopped there while migrating at the start of the dry season and a juvenile from the delta did so early in the wet season while in transit to the Northern Plains. In the Mekong Delta, the early dry season foraging habitat at Boeung Prek Lapouv has long been known and is protected. When conditions became too dry at Boeung Prek Lapouv in January or February, tagged cranes moved to Anlung Pring, where they made daily movements within the site, or to Phu My (protected) or Phnom Teuk (unprotected), both being wetlands near Anlung Pring. However, one of the 2 families tracked in 2015 made a sudden departure to recently harvested rice fields (in Kien Luong) for several weeks, along with a total of 91 cranes counted there during a follow-up visit, while a family from Tram Chim in 2001 utilized harvested rice fields in April that were adjacent to Tram Chim National Park. These records indicate that harvest residues, when located near wetlands appropriate for roosting, are important food sources in the delta as well as in the Tonle Sap floodplains.

4.2. Wet season movements

4.2.1. Breeding adults

Adults from the Tonle Sap floodplains moved to locations in the Northern Plains during the wet season while those from the Mekong Delta moved to either the Eastern or Northern Plains. The cranes appeared to minimize the distance between breeding and non-breeding areas if suitable nesting habitat could be found. Kulen Promtep and Chep were previously known to be important crane nesting areas in the Northern Plains (Clements et al. 2013), and their presence in the wet season had been con-

firmed from various locations within the deciduous dipterocarp forest range in the Eastern and Northern Plains of Cambodia (van Zalinge et al. 2023), but linkages to dry season sites were not known. Territories located within some protected areas in Cambodia may benefit from a degree of protection (Clements & Milner-Gulland 2015), but the area between Kulen Promtep and Beng Per has been undergoing conversion to plantations and is otherwise rapidly being settled by small landholders. Such conversion to plantations was also occurring in the area southwest of Chep, used by a tracked juvenile in 2015 and 2016 and an adult in 1998, as well as areas used in Lomphat and Seima Wildlife Sanctuary in the Eastern Plains. Presently, Cambodia is undergoing rapid deforestation (Davis et al. 2015), particularly in the north and northeast (Pacheco et al. 2021).

4.2.2. Juveniles

The movements of juveniles after becoming independent from their parents were unpredictable. In 2001, 2 juveniles from the same family moved north with their parents and stayed near their parents' breeding territory, whereas in 2015, all of the juveniles separated from their parents while in dry season habitats or soon after reaching wet season habitats. Similar variation in the timing of disassociation of juveniles from their parents has also been observed with sandhill cranes in the USA, where almost 10% of juveniles returned to breeding grounds with their parents while around 70% had already disassociated in non-breeding areas (Hayes & Barzen 2016b). With sandhill cranes, the timing of disassociation did not influence survivorship, but it may have with sarus cranes. Large and unpredictable home ranges for sub-adults are also known from sandhill cranes (Hayes & Barzen 2016a, Wolfson et al. 2020), as was the case in this study.

That 2015 had such a long dry season may have also caused juveniles to stay longer in the floodplains and travel more extensively, with some making several flights between upland and floodplain regions. It is not only the distances covered but the irregular behaviour of these inexperienced cranes that differs from that of adults. Often juveniles made unsafe choices, using agricultural areas near villages. When they eventually moved to upland regions after the onset of the rainy season, 1 tagged juvenile, in a group with 6 other juveniles, selected flooded rice fields in the upland region of Varin where the crop had failed and been abandoned. Two other tagged juveniles that also used agricultural areas in the wet season fared poorly and were captured by people. The unpredictable behaviour of juveniles complicates explicit spatial planning for strengthening the protected area network, instead emphasizing the need to alter attitudes among people in the wider landscape used by cranes so that the birds are less likely to be captured or hunted.

4.3. Habitat protection within floodplains

While much important non-breeding habitat is within protected areas in Cambodia and Vietnam, this study identified 2 staging sites in the Tonle Sap floodplain where protection is lacking: Preah Net Preah and Santuk. The Tonle Sap floodplain may also contain other scattered small wetlands used by families and other small groups similar to those at Stoung. At Stoung itself, cranes benefit from active patrolling and raising community awareness associated with the presence of the Critically Endangered Bengal florican *Houbaropsis bengalensis* (Gray et al. 2009). Starting with Preah Net Preah and Santuk, measures that protect cranes and biodiversity in general across the wider landscape will need to be developed in collaboration with private landowners and other stakeholders. This is especially true given interannual variations in flooding and rainfall patterns, with safe access to forage across multiple sites, even those not used every year, likely to become increasingly important for crane conservation in the floodplain. The mosaic of wetlands, grasslands and rice fields found in the Tonle Sap floodplains of high value to the Bengal florican (Gray et al. 2007) are rapidly disappearing (Packman et al. 2013), with a significant increase in the cultivation of dry season rice (Ibbett et al. 2019, Mahood et al. 2020). It is similarly important to ensure cranes can use the rice fields surrounding Ang Trapeang Thmor safely so that they continue to have access to leftover grain. Where sarus cranes are not persecuted, such as in parts of India and Myanmar (Archibald et al. 2003) and the site of a reintroduction project in Thailand (N. Purchkoon pers. comm.), cranes can successfully use the agricultural landscape, even nesting within inundated rice paddies.

4.4. Resightings and mortality

One out of the 5 adults tagged in 2015 was not resighted at the main dry season sites, Anlung Pring,

Ang Trapeang Thmor or Stoung, in 2016–2017. This was similar for cranes caught in 1998 or 2001, over a 2 yr period following initial capture. Although our sample size is small, our adult mortality rates would be unsustainable for most other long-lived crane populations that have been studied (Sæther & Bakke 2000, Servanty et al. 2014).

Threats to juvenile cranes are also substantial. Of the juveniles tracked, 60% probably either died or would have done so without intervention by the research team. Transmission from 1 individual ended abruptly in southwest Seima Wildlife Sanctuary, but its fate is unknown. The other 2 were caught by people: one by wildlife traders and another, in a weakened condition, by farmers. Re-sighting data of juveniles from dry season sites across the different study periods suggests that 45% of all juveniles that had successfully migrated with their parents from natal areas to dry season grounds did not return the following dry season, or subsequently. The mortality rate of sandhill cranes, reported from a population at carrying capacity in the USA, was 18% in their first year and 11% in their second (Wheeler et al. 2019). Although our sample size is small, this suggests that survival of juvenile cranes in Cambodia and/or Vietnam is lower than that in the USA, mostly as a result of direct encounters with people.

Lastly, of the 4 adult pairs returning from the breeding grounds to dry season sites in 2015–2016, only one, at Anlung Pring, was accompanied by a single new juvenile. The one adult confirmed to have nested, with a single egg that hatched, arrived at Ang Trapeang Thmor without an accompanying juvenile. A low level of recruitment and high adult mortality in the wet season is consistent with long-term monitoring suggesting rapid population decline (van Zalinge 2022) and indicates that breeding cranes need greater protection.

5. CONCLUSIONS

Tracking of the eastern subspecies of sarus crane has identified 2 main movement patterns between breeding and non-breeding sites. One sub-population migrates between breeding sites east of the Mekong River (Eastern Plains), extending to the eastern Northern Plains and non-breeding sites in the Mekong Delta. The other migrates between breeding sites in the west-central Northern Plains and non-breeding areas on the northern Tonle Sap floodplain, including Ang Trapeang Thmor. Tracking identified 2 new and important early dry-season stop-over sites in the Tonle Sap floodplains for cranes migrating from the Northern Plains: Santuk, for those moving to the Mekong Delta, and Preah Net Preah, for those moving to Ang Trapeang Thmor. While most of the sites used in the Mekong Delta have a protected status, significant sites in the Tonle Sap floodplain, such as Preah Net Preah and Santuk, lack any form of protection, making them highly vulnerable to conversion to intensive agriculture and unsafe for cranes. More floodplain habitat requires management for multiple purposes, including humans, cranes and the maintenance of biodiversity.

High mortality and low reproductive success suggest that mortality due to hunting/capture is a major issue, particularly during the wet season. Direct evidence of nest disturbance (chick) and capture for the wildlife trade (juvenile) was found. The loss of adults is of major concern, and stronger protection of breeding habitat is required, including areas in and around Lomphat, Kulen Promtep and Chep Wildlife Sanctuaries. Strengthening deciduous dipterocarp forest protection, particularly small, scattered wetlands that lie within the forests between Kulen Promtep, Beng Per and Chep, is likely to be particularly beneficial. Aerial surveys should be conducted during the main nesting period to identify more active territories, prioritizing the areas mentioned above.

Our sample size remained small, and more tracking of adult cranes would help identify additional breeding areas and their linkages to the Tonle Sap and Mekong Delta sub-populations as well as enhance our understanding of the dry season distribution as agricultural intensification and climate change alters habitat suitability. Banding more cranes, especially juveniles, and improving the recording of re-sightings will also help improve our understanding of the population dynamics of this vulnerable species.

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