Spatial ecology of freshwater eels in South Africa: Implications for conservation

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Declarations

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Conflicts of interest

The authors have no conflict of interests.

Availability of data and material

Research data may be obtained from the lead author upon reasonable request. The code used for home range analysis (PHRE) has been developed by Max Tarjan and is freely available on GitHub (https://github.com/mtarjan/PHRE/blob/master/PHRE_eel.R)

Abstract

Four freshwater eel species (*Anguilla* spp.) occur in southern African rivers that are increasingly anthropogenically modified. Information on movements, habitat use and overlap by African eels is needed for their conservation. We carried out a preliminary investigation of the spatial ecology of three eel species in the Thukela River, South Africa, using radio-telemetry. Nineteen yellow-stage eels were surgically implanted with radio-tags, comprising *A. mossambica* (*n* = 2), *A. bengalensis* (*n* = 9) and *A. marmorata* (*n* = 8), and tracked from October 2018 to August 2019. Tagged eels exhibited high individual variability in space use. We recorded very small home ranges in winter for all species. A lack of apparent territoriality at inter- and intra-specific levels was observed. Eel species tended to use similar mesohabitats, especially glides, but habitat preference changed across seasons, and between species, suggesting fine-scale spatial and temporal niche partitioning. Given the breadth of flow typologies used by Thukela eels across the seasons, conservation of these long-lived species indicates that management of river flows needs to be sensitive to their habitat requirements all year round, but in many water-stressed South African rivers, this may be unlikely. Maintaining good habitat connectivity for these migrant species must be prioritised.

Keywords Radio-telemetry; *Anguilla*; home range; habitat use; water resource management; rivers

Introduction

Freshwater eels (*Anguilla* spp.) are catadromous, migratory fishes that are indicators of river continuity and are flagship conservation species occurring around the globe (Jacoby et al., 2015). The abundance of several temperate eel species has declined dramatically in recent decades, with river habitat degradation and damming believed to contribute substantially to their decline (Dekker, 2003; Castonguay & Durif, 2015; Jacoby et al., 2015). Similarly, the less studied “tropical eel” (*sensu* Jacoby et al., 2015) species are facing similar threats. The biology of most of these tropical eel species is poorly known, and most are probably undervalued ecologically and commercially. Tropical eel species may be at risk of endangerment if the present trends of habitat deterioration and fragmentation (Hanzen et al., 2019), and biological exploitation (Jacoby et al., 2015; Hanzen et al., 2019), continue.

Four eel species occur in the Western Indian Ocean Region; the African longfin eel *Anguilla mossambica* (Peters, 1852), the African mottled eel *A. bengalensis* (Gray, 1831), the shortfin eel *A. bicolor* McClelland, 1844 and the giant mottled eel *A. marmorata* Quoy & Gaimard, 1824 (Skelton, 2001; Hanzen et al., 2019). African river systems are increasingly threatened by anthropogenic habitat degradation, pollution, damming and water diversion (Mantel et al., 2017; O’Brien et al., 2019). Of particular concern is the case of the African endemic *A. mossambica*, the conservation status of which was recently changed from “Least concern” to “Near threatened”, partly because of the worrying decline in range distribution in KwaZulu-Natal, South Africa (Pike et al., 2019). Information is urgently needed on these species' habitat use and behaviour, including the extent to which they may share habitats, to develop sustainable water management practices and conserve remaining eel populations (Hanzen et al., 2019).

The yellow eel stage, during which eels grow towards maturity in fresh or coastal waters, can last between 7 and 50 years depending on the species, sex and geographic location

(McEwan & Hecht, 1984; Tesch, 2003). Widespread seasonal movements of several eel species between freshwater, estuaries and the sea have been shown by otolith microchemistry (Arai & Chino, 2012) and by telemetry (Thibault et al., 2007). More localised movements between habitats can be exhibited by eels residing in the lower reaches of river systems (Daverat et al., 2006; Lin et al., 2015). Preferences for riverine habitats may vary between eel species and also size classes, with large individuals usually found in large, deep pools and smaller individuals in shallow, faster-flowing habitats (Valade et al., 2018). However, where several species of riverine eels occur within the same catchment and use similar habitats, they may exhibit local differences in mesohabitat use or feeding habits (Lecomte-Finiger, 2003; Robinet et al., 2007), or exhibit differences in diel or seasonal activity, as for sympatric eel species in New Zealand (Jellyman & Sykes, 2003). In rivers, once yellow eels have settled in a locality, they are generally considered to be sedentary, as observed for the European eel *Anguilla anguilla* (Linnaeus, 1758) (Ovidio et al., 2013), and *A. dieffenbachii* Gray, 1842 and *A. australis* (Richardson, 1841) in New Zealand (Jellyman & Sykes, 2003). Eels can also exhibit strong homing behaviour (Thibault et al., 2007) and even a strong fidelity to a particular bank (Jellyman & Sykes, 2003).

In South Africa, Lin et al. (2015) observed that *A. mossambica* and *A. marmorata* spent most of their time in freshwater with a few sporadic episodes back to brackish environments. In riverine environments, the four tropical African eel species exhibit a degree of longitudinal zonation at the catchment scale, with *A. mossambica* being the most ubiquitous species found throughout catchments (Hanzen et al., 2019). Differences in longitudinal distribution translate into putative differences in habitat use for the four species, with *A. bicolor* usually found in coastal swamps, the lower reaches of rivers and coastal lakes, while the other species occur in all available riverine habitats (Jubb, 1961).

This preliminary study focused on the home range (the area used by an animal for daily activities; Burt, 1943) and habitat use of three freshwater eel species during their riverine phase in the Thukela River, South Africa. Due to its preference for coastal areas and its rarity, the fourth eel species *A. bicolor* was not included in the present study. We hypothesised that the three eel species present (*A. mossambica*, *A. marmorata* and *A. bengalensis*) would exhibit (1) limited home ranges and core area; (2) different preferences regarding habitat use; and (3) different seasonal activities. We predicted small home ranges in winter. We expected overlaps in home range and core area between individuals and sympatric species. We discuss the outcomes in the context of river management in South Africa and the conservation actions needed to safeguard these eel species' future in Africa.

Materials and methods

Study area

The Thukela catchment is the largest in KwaZulu-Natal Province, South Africa, (30,000 km^2 (DWAF, 2002)) and flows from the Drakensberg Mountains for about 500 km before ending in the Tugela Mouth in the Indian Ocean (Fig. 1). The Thukela River is highly dynamic, with substantial differences in water levels between the low flow season during the austral winter (June-August) and the high flow season (December-February) during the austral summer. Water temperature ranges from ~8°C to ~29°C with average daily temperatures of ~24°C in summer and of ~12°C in winter (recorded in 2018-2019). The few major impoundments located in the catchment are found mostly in the headwaters (Fig. 1). The Umgeni Water Bulk Transfer Weir in the lower river was built in 2017 and is equipped with a vertical slot fish ladder (12% slope) and a creeper wall, both designed to allow upstream eel passage.

Our study area was a 6 km river reach, located at Zingela, a private nature reserve (Fig. 1), ~300 km upstream from the river mouth. The Zingela portion of the Thukela has a range of lotic habitats, including deep pools, and faster shallower habitats with rocky substrates, with at least three African eel species present (*A. mossambica*, *A. marmorata*, *A. bengalensis*). Our study locality included larger areas of glides and pools that were generally deep (>5 m) and where the substrate was mainly composed of relatively large boulders, possibly providing good cover. While cover is usually a way to minimise predation, it should be noted that relatively few predators are present in the Thukela River. Historically, they included Nile crocodiles *Crocodylus niloticus* Laurenti, 1768, which are now relatively rare and only present in the summer months (P. Calverley pers. obs.), and various otter *Aonyx* spp. that were observed to prey on eels in KwaZulu-Natal Province (Rowe-Rowe, 1977) and Zimbabwe (Butler and du Toit, 1994). Our study area's river water was relatively turbid all year round, with a visibility of less than 0.5 m, making any visual observations of eel behaviour in mesohabitats very difficult. The region is characterised by annual precipitation ranging between 600 to 1000 mm, mainly occurring in the austral summer (December - February) (Kleynhans et al., 2005), although the rainy season usually starts from October.

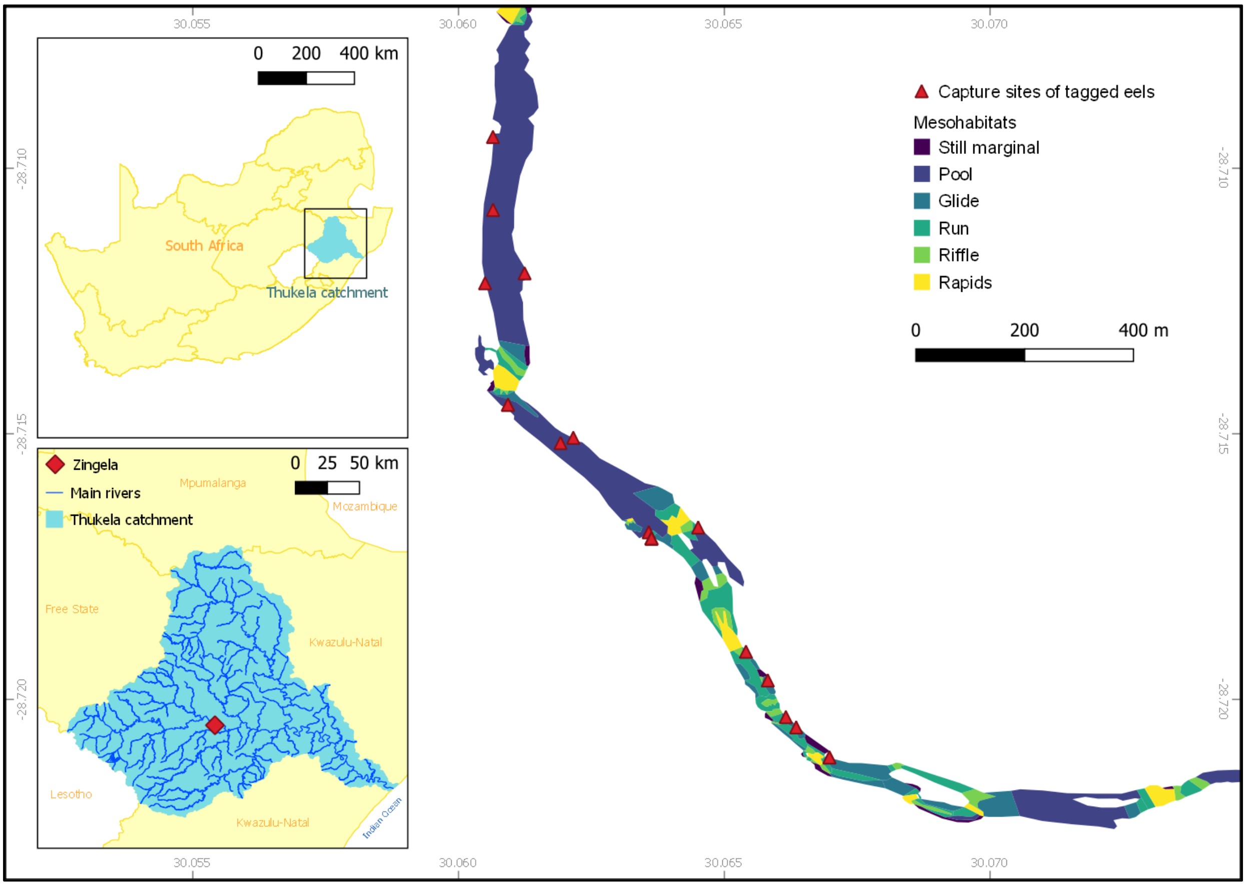

Fig. 1 The study area, a 3-km stretch of the Thukela River, at Zingela, KwaZulu-Natal Province, South Africa. The sites of capture for the tagged eels are also shown on the map.

Capture and tagging

Radio-telemetry is regarded as a suitable technique to determine larger fish's spatial ecology in African systems (Økland et al., 2007; Burnett et al., 2020) and an effective method for studying eel movements in freshwater ecosystems (Béguer-Pon et al., 2018). Therefore, we chose to use telemetry for this study. We obtained permission from the University of KwaZulu-Natal Animal Ethics Committee (AREC/012/017D). We captured eels from October 2018 to January 2019 using commercial fyke nets (*n* = 8-12, 19 mm mesh, opening height 60 cm, T & L Netmaking, Mooroolbark, Australia) during at least six consecutive nights per month. Eels of all three study species and the sizes needed for tagging were not abundant, and this limited the sample size available for study. Captured eels were anesthetised using 2-phenoxyethanol

(0.5 ml/l) in river water. We identified the individual to the species, weighed and measured each individual. We used the distance between the dorsal fin origin and anus/gill slit to differentiate the species (Skelton, 2001). Radio tags (Advanced Telemetry Systems Inc., Isanti, USA, 40 MHz, trailing whip antenna, model F5180, weight ~3.6 g, length ~24 mm and 284 days minimum battery life; model F1820, weight ~9.5 g, length ~36 mm and 286 days minimum battery life) were surgically implanted in the abdominal cavity through a ~2 cm mid-ventral incision (following Ovidio et al., 2013), at a position of 25-30% of body length from the snout, to minimise proximity to vital organs and the probability of eels biting the sutures (following Økland and Thorstad, 2013). We took the trailing antenna through the abdominal wall with a hollow needle. The incision was closed with three separate sutures (CliniSolv 8224RC 24 mm 3/8 Circle Reverse cutting Monofilament Synthetic Absorbable Suture, Port Elizabeth, South Africa). A post-surgery risk of infection was a concern because several water quality issues have been observed in the catchment (including high nutrient concentrations and faecal microbes (DWS, 2019). For that reason, while the use of antibiotic has become controversial (Mulcahy, 2011), all tagged eels were administered Terramycin® (Zoetis, Sandton, South Africa) containing oxytetracycline (1ml/kg), intramuscularly. Wound gel care (Aqua Vet, Lydenburg, South Africa) was applied to the incision site to reduce potential inflammation (Burnett et al., 2020) and to help protect the wound from biting and friction with the substrate. Eels were placed in a 50-L bucket containing aerated fresh river water, monitored, and released back at their capture site less than 1 h after surgery. The tagging method used, and its validation, are described extensively in Hanzen et al. (2020).

Tracking

We tracked tagged individuals from the riverbank or a kayak using a wideband receiver Alinco DJ-X10 (Alinco, Osaka, Japan) with a Yagi antenna using a combination of triangulation and the gain reduction method, depending on location (Cooke et al., 2012). Blind tracking tests beforehand showed that error in tag location was less than 5 m. At river level, detection range was 200-300 m depending on habitat, and up to 1000 m when tracking from higher ground. Tagged eels were tracked daily from October 2018 to January 2019, then daily for 10-15 consecutive days monthly from February to September 2019. Tracking sessions (n = 201) were conducted following a random stratified pattern at dawn (n = 35), day (n = 78), dusk (n = 58) and night (n = 30). We defined dawn and dusk periods as 1.5 h before and after sunrise or sunset. For safety reasons because of hunting parties, poachers, dangerous wildlife, high water levels and fires, tracking sessions were flexible, and night tracking had to be reduced in frequency and conducted only when feasible.

We created a high-resolution digital map of the Zingela reach from drone footage and used this to record tagged eel locations. Four drone flights (DJI Mavic 2 Pro, Shenzhen, China) were automated and programmed beforehand using Litchi (Litchi for DJI Drones 2.6.3, VC Technology Ltd, flylitchi.com) to capture our study area (150 photographs, elevation 135 m). We created the digital map with QGIS 2.8 (QGIS Geographic Information System. Open Source Geospatial Foundation Project, qgis.osgeo.org) and used this on a Vanquisher Ultra Rugged tablet (Sinicvision Handhelds & Mobility Co., Ltd, Shenzhen, China) to allow the mapping of precise locations of tracked eels *in situ.* Mesohabitats were also recorded. We used all geographic coordinates of tracked eels to analyse home range, spatial overlap and habitat preferences.

Home range and core area utilisation

We analysed home ranges of individual eels using the Permissible Home Range Estimation (PHRE), developed by Tarjan and Tinker (2016). While conventional home range analyses do not take inaccessible habitat into account, the PHRE function has been developed to model home range of species that use restricted habitats, in R 3.6.0 (R Core Team, 2019). We created a shapefile of the river in QGIS 2.8 from the digital map. It was then converted to an array of points (5 m x 5 m) where its distance located each of the points to the bank and their longitudinal position along the river. The river habitat in a landscape coordinate system was then integrated using the PHRE function in R 3.6.0. This function (1) transformed all tag locations into the newly created landscape coordinate system, (2) calculated kernel density estimates within that landscape and (3) back-transformed these probabilities into a geographic coordinate location system. We calculated space use of each tagged eel at 90% (home range) and 50% (core area) probability distributions for the study duration and per season.

We defined seasons according to the four austral seasons: spring from September to November with sporadic rain, summer from December to February, which corresponded with the rainy season, autumn from March to May with sporadic rain, and finally winter from June to August, the dry season. We analysed seasonal differences in home range and core area sizes and compared species using the Kruskal–Wallis (KW) test followed by a paired comparison Mann–Whitney (U) test. For all statistical analyses, significance was set at $P < 0.05$. Only small numbers of comparisons were made, so Bonferroni corrections were not applied. As only two individuals of *A. mossambica* were tracked, no statistical analyses were performed for this species.

We estimated spatial overlap for home ranges using statistical analyses following the methods of Kernohan et al. (2001). The overlap (HR_{ij}) is the proportion of the home range of individual i shared with individual j, where A_{ij} is the area shared by two individuals i and j and A_i is the home range of individual i. Traditional longitudinal home ranges (Cooke et al., 2012) were also estimated for each individual by calculating the distance between the most upstream and most downstream location. Additionally, we used generalised linear modelling (GLM) approach to test the effect of home range and the distance between the capture locations on the home range shared area. We incorporated a Gaussian distribution into these models. Finally, we used regression analyses (simple linear and power functions) to analyse the relationships between home range and body mass for *A. bengalensis* and *A. marmorata*. Based on these results, we also used GLM to analyse the interaction between body mass and seasonality on the home range depending on seasons. A gamma distribution with an inverse link function was incorporated into these models. For all GLM analysis, the goodness of fit of the different models was evaluated with a Kolmogorov-Smirnov test using the DHARMa package (R Core Team, 2019).

Habitat use

We created a map of the mesohabitats (pool, glide, run, riffle, rapids, still marginal) from observations during the austral spring, in October 2019 (intermediate discharge). The mesohabitat definitions are described in Supplementary Information Table S1. Although river flows were variable, the mapped mesohabitats did not change substantively seasonally, during checks across seasons. Seasonal variation and use per species were analysed using Pearson's Chi-squared test (χ^2) with the simulated p-value. Mesohabitat selection was evaluated using the Ivlev Electivity Index E_1 (Ivlev, 1961): $E_1 = \frac{r_i - n_i}{r_i + n_i}$ where r_i is the percentage of habitat *i* used by one individual and where n_i is the percentage of habitat *i* available in the study area. The electivity index varies from -1 (complete selection against) through 0 (no selection) to +1 (complete selection towards). Results for *A. mossambica* were included here; however, they should be considered with caution as only two individuals were tracked.

Table 1 Tracking data for all eels tagged, including the total length (mm), body mass (g), tag mass ratio (% of body mass), duration of tracking, number of observations per individual in the present study and final fate of the fish.

ID	**Species**	**Total length (mm)**	**Body mass (g)**	**Tag mass ratio (%)**	**Tracked**		**Fate of the tagged fish**	**Observations (*n*)**
					from	**to**		
1	*A. mossambica*	650	855	0.4	23/10/2018	23/08/2019	Still transmitting 23/08/2019	152
2	*A. mossambica*	570	480	0.8	23/01/2019	23/08/2019	Still transmitting 23/08/2019	56
3	*A. marmorata*	1300	4700	0.2	25/10/2018	21/06/2019	Last detection on 21/06/2019	142
4	*A. marmorata*	1380	7800	0.1	25/10/2018	23/08/2019	Tag expelled in Dec 2018, retagged and still transmitting 23/08/2019	131
5	*A. marmorata*	1180	4200	0.1	28/10/2018	23/08/2019	Still transmitting 23/08/2019	159
6	*A. marmorata*	770	955	0.4	20/11/2018	23/08/2019	Still transmitting 23/08/2019	114
7	*A. marmorata*	1270	5100	0.2	21/11/2018	22/06/2019	Last detection on 22/06/2019	100
8	*A. marmorata*	1010	2080	0.2	22/11/2018	20/06/2019	Last detection on 20/06/2019	92
9	*A. marmorata*	700	765	0.5	05/12/2018	26/01/2019	Located out of Zingela study area	18
10	*A. marmorata*	1450	6970	0.1	24/01/2019	22/03/2019	Last detection on 22/03/2019	21
11	*A. bengalensis*	1250	4550	0.2	27/10/2018	16/06/2019	Last detection on 16/06/2019	130
12	*A. bengalensis*	1190	4045	0.2	20/11/2018	22/06/2019	Last detection on 22/06/2019	107
13	*A. bengalensis*	770	820	0.4	22/11/2018	23/08/2019	Still transmitting 23/08/2019	107
14	*A. bengalensis*	955	1630	0.2	22/11/2018	23/08/2019	Still transmitting 23/08/2019	98
15	*A. bengalensis*	910	1650	0.2	23/11/2018	23/08/2019	Still transmitting 23/08/2019	102
16	*A. bengalensis*	850	1485	0.2	04/12/2018	23/05/2019	Last detection on 23/05/2019	76
17	*A. bengalensis*	1090	3040	0.3	24/01/2019	23/08/2019	Still transmitting 23/08/2019	57
18	*A. bengalensis*	1210	3435	0.3	27/01/2019	18/08/2019	Last detection on 18/08/2019	50
19	*A. bengalensis*	1260	5680	0.2	27/01/2019	22/06/2019	Last detection on 22/06/2019	41

Results

We caught a total of 38 freshwater eels using fyke nets in the study area between October 2018 and January 2019 (*A. bengalensis* $n = 15$; *A. marmorata* $n = 12$; *A. mossambica* $n = 11$), with size ranging from 215 to 1450 mm and body mass from 120 to 7900 g. From October 2018 to August 2019, we collected a total of 1752 location data for 19 tagged eels comprising two *A. mossambica*, eight *A. marmorata* and nine *A. bengalensis* (Table 1). A total of 277 locations were recorded at dawn, 758 during the day, 485 at dusk and 232 at night (see summary in Supplementary Information Table S2). Until 8 January 2019, all tagged individuals were located in our study area. On this date, individual #9 (*A. marmorata*) was located outside of the study area. Eel #9 did not return to Zingela. At the end of the study in August 2019, 47% of the tagged individuals ($n = 9$) were still transmitting. Location data per individual ranged from 18 to 152 data points, corresponding respectively to 52 and 304 days after tagging (Table 1). Seven eels were recaptured, all displaying an advanced or complete state of healing. Two cases of tag expulsion were suspected (individuals #4 and #15). This was confirmed for individual #4 (based on size and location), which was retagged and remained active until the end of our study. Recapture rate, wound healing and validation of internal tagging for freshwater eels in South African rivers are detailed in Hanzen et al. (2020).

Home ranges and core areas

Individual home range (90% PHRE) and core area (50% PHRE) for all tagged eels are presented in the Supplementary Information Figs S1-S3. High individual variability was observed, with home range size ranging from 1 863 m^2 to 36 166 m^2 (Supplementary Information Figs S1-S3) for the entire study period. All individuals exhibited one or more restricted core areas, representing 4.9% to 38.6% of the home range size and ranging from 375 m^2 to 11 055 m^2 (combined core areas, Fig. 2). No significant differences were observed for median home range size nor core area between *A. marmorata* and *A. bengalensis* (Mann-Whitney *U*, home range, P = 0.7; core area P = 0.8) with similar home range medians of 15 459 m^2 and 13 239 m^2 respectively, and similar core area medians of 3 472 m^2 and 3 645 m^2 respectively. All statistical results have been summarised in the Supplementary Information Table S3. Maximum home range for *A. marmorata* was 36 166 m^2 with a core area of 11 055 m^2 (30.5% of home range) and 28 792 m^2 for *A. bengalensis* with a core area of 9060 m^2 (31.4% of home range). Both *A. mossambica* individuals exhibited relatively larger home ranges of 32 432 m^2 with a core area of 9764 m^2 (30.1% of home range), and 25600 m^2 with a core area of 6 098 m^2 (23.8% of home range), for each individual.

Linear home ranges ranged from 85 to 2340 m with a median of 495 m for *A. bengalensis*, 695 m for *A. marmorata*. Two *A. marmorata* individuals, #4 and #9, exhibited relatively large longitudinal home ranges of 2 340 m and 2 110 m respectively, although these can be attributed to large single excursive movements of each outside of their normally used areas.

The relation between body mass and home range (90% PHRE) for *A. bengalensis* was best explained through a power relationship (R^2 = 0.52, P = 0.02, Fig. 3). No significant relationships were observed between body mass and home range, core area, nor longitudinal home range for *A. marmorata*.

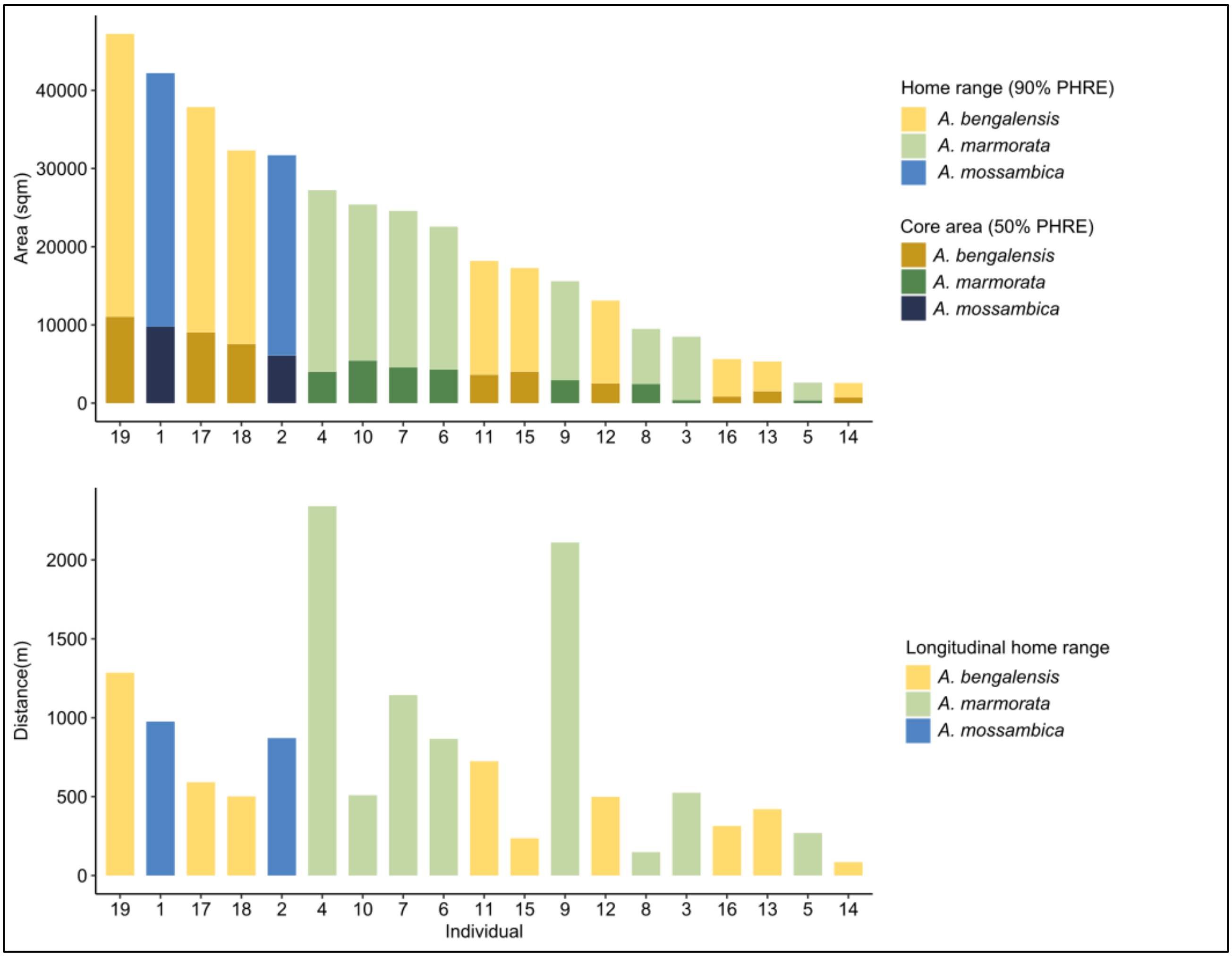

Fig. 2 Home range size (90% permissible home range area, PHRE – see main text) and core area (50% PHRE) for each individual eel (in m^2, upper panel) and linear home range (in m, lower panel) in the Thukela River, South Africa (See Table 1 for individual information). The large linear home ranges for individuals #4 and #9 are because of excursions.

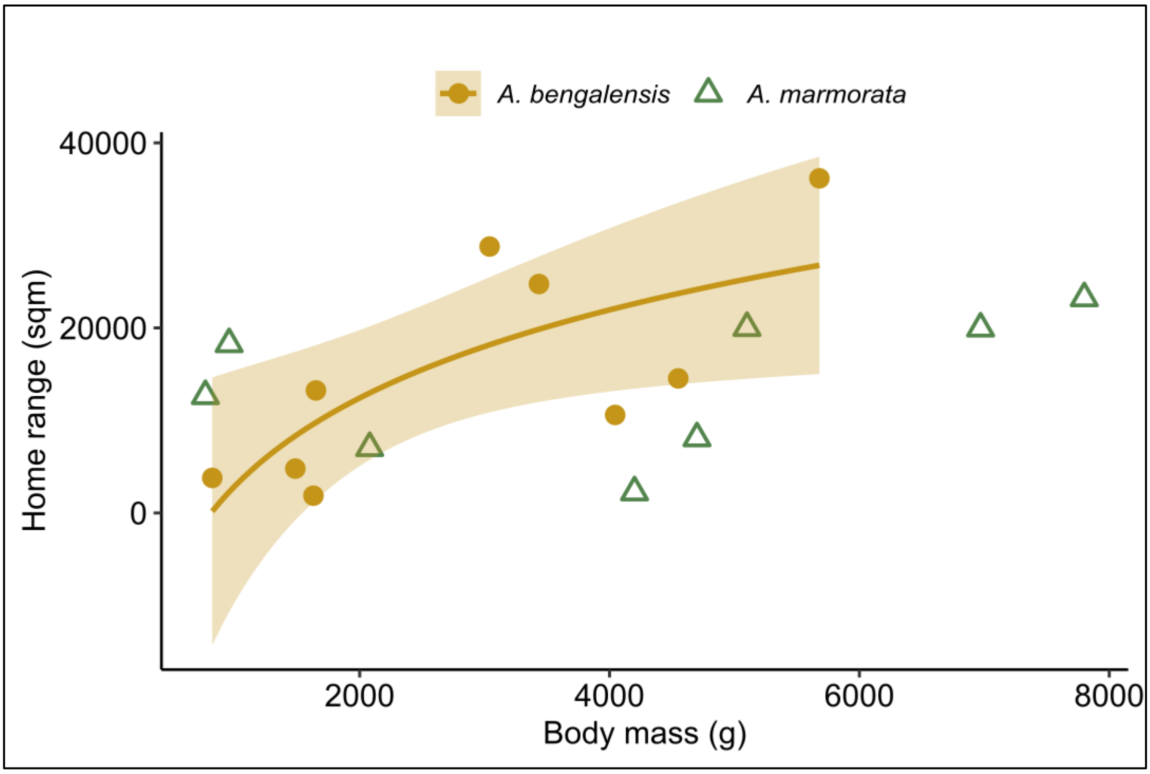

Fig. 3 Relationships between body mass and home range size (90% PHRE) for *A. bengalensis* (including the line of best fit) and *A. marmorata* (no relationship) in the Thukela River, South Africa.

Seasonality in home range and core area

Anguilla bengalensis home range (90% PHRE) size varied with season (Kruskal-Wallis, $P = 0.06$, nearly significant, see the summary of statistical results in Supplementary Information Table S3), with winter home range size significantly smaller than summer (Mann-Whitney U, $P = 0.03$) and autumn (Mann-Whitney U, $P = 0.02$; Fig. 4). The same trend was observed for *A. marmorata* (Kruskal-Wallis, $P = 0.03$) with a smaller home range size in winter (Mann-Whitney U, vs spring, $P = 0.01$; summer, $P = 0.01$; autumn, $P = 0.02$). No significant differences in home ranges occurred between spring, summer and autumn for these species. *Anguilla mossambica* had a relatively large home range size in summer, 225 260 m^2 for individual #1 and 19 101 m^2 for individual #2, compared with 819 m^2 and 343 m^2 respectively in winter (Fig. 4).

Both *A. bengalensis* and *A. marmorata* exhibited seasonal differences in core area (50% PHRE) size (Kruskal-Wallis, $P = 0.01$ and $P = 0.03$ respectively), the species having the smallest medians in winter of 112 m^2 and 418 m^2 respectively (Fig. 4). No significant seasonal differences occurred in core area between the other seasons for these species. Some tagged individuals were located at the same location for weeks in winter showing reduced activity and movements during this period.

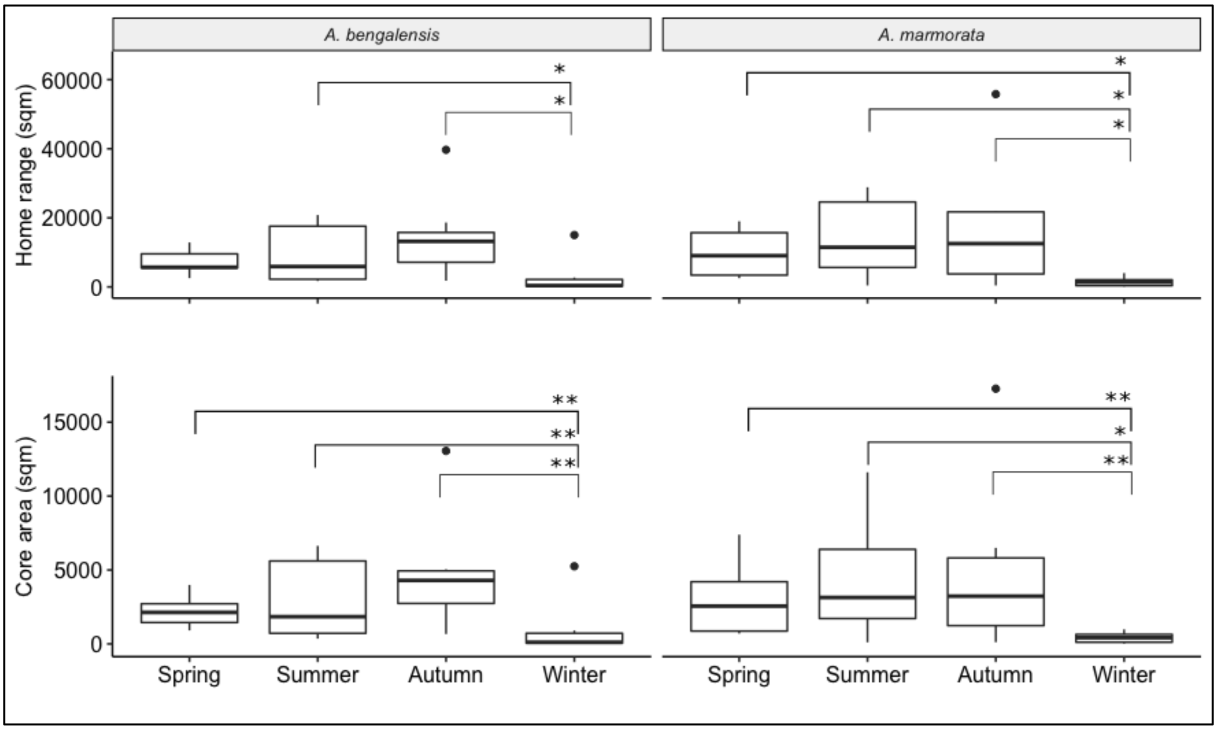

Fig. 4 Box plots of home range and core area (m^2) for the eel species *A. bengalensis* and *A. marmorata* in spring, summer, autumn and winter in the Thukela River, South Africa. Levels of significance between seasonal paired values represented by * ($P \leq 0.05$), ** ($P \leq 0.01$)

As the effect of the body mass on the size of the home range has been observed for *A. bengalensis* (Fig. 3), we analysed the two-way interaction between eel body mass and season on home range size. Results from GLM analyses (Supplementary Information Table S4) showed no significant interaction effect between these covariates.

Home range overlap

No eels exhibited exclusive use of their home range areas, with overlaps observed for all tagged individuals at both inter- and intraspecific level (Fig. 5). Home range was shared on average with six individuals for *A. mossambica*, three for *A. marmorata*, three for *A. bengalensis* and reached a maximum of eight individuals for one *A. marmorata*. At the intraspecific level, *A. bengalensis* and *A. marmorata* shared their home range with two individuals on average and a maximum of five and three, respectively. The two species shared their home range equally with conspecific and heterospecific individuals (Mann-Whitney *U*, $P = 0.97$ for *A. bengalensis*, $P = 0.91$ for *A. marmorata*).

Core area overlap occurred for 63.2% of individuals. Three (15.8%) individuals did not share their core area at the interspecific level and four (21%) at the intraspecific level. *Anguilla mossambica* exhibited greater overlap in terms of the number of individuals, with a mean of six individuals, followed by *A. marmorata* and *A. bengalensis* with a mean of two individuals each sharing their core area and a maximum of five and three, respectively (Fig. 5). *Anguilla marmorata* showed a slightly greater overlap in core area with conspecifics than heterospecifics (Mann-Whitney *U*, $P = 0.06$) while *A. bengalensis* shared core area equally with con- and heterospecific individuals (Mann-Whitney *U*, $P = 0.57$).

The size of the shared home range of tagged eels was found to be slightly positively influenced by the size of the home range (GLM, $P < 0.001$; Supplementary Information Table S5) and negatively influenced by the capture distance (GLM, $P = 0.02$) for *A. bengalensis*. For *A. marmorata*, only the size of the home range seemed to have a positive effect on the home range shared area (GLM, $P = 0.004$). Analyses for core are were not performed as not all tagged eel exhibited overlap in their core area.

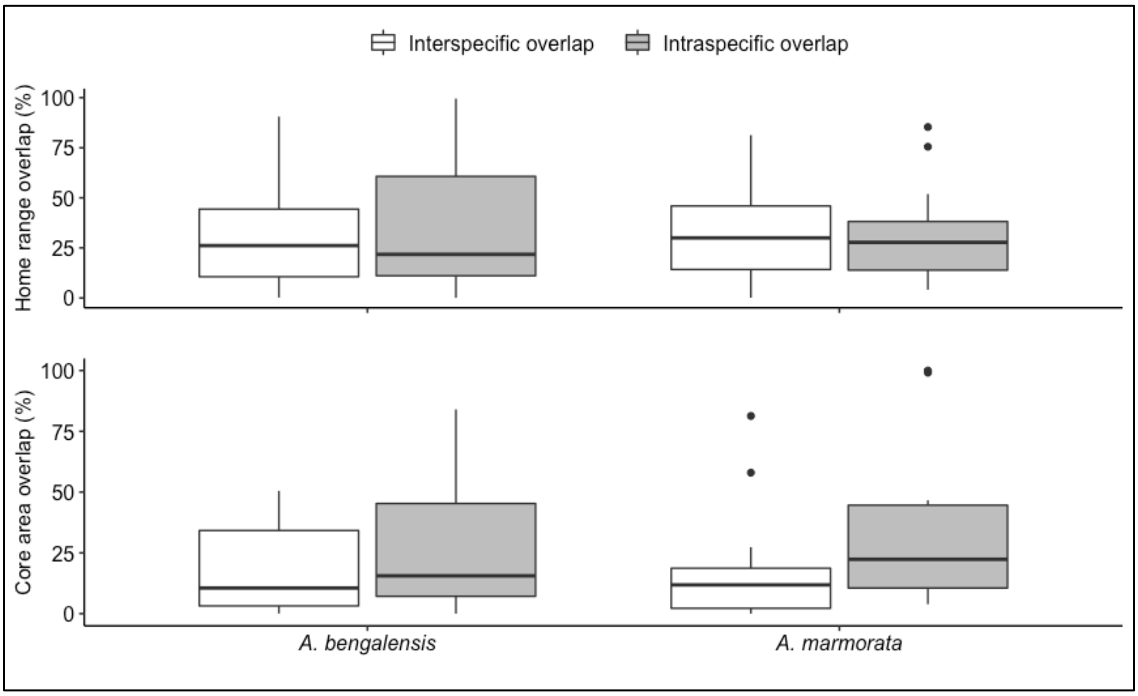

Fig. 5 Home range and core area overlap (% of area) for the tagged *A. bengalensis* and *A. marmorata* in the Thukela River, South Africa. Both species were found to share their home range and core equally with con- and heterospecific individuals.

Habitat use

In the study area, mesohabitats were comprised mostly of pools (58% of habitat available), followed by runs (14%) and glides (13%) (Fig. 1). Rapids (7%), riffle (6%) and still marginal (2%) habitat were less represented. *Anguilla marmorata* and *A. bengalensis* used all biotopes available, with higher use of pools (33% and 40% respectively) and glides (31% and 41% respectively), while *A. mossambica* was mostly restricted to pools (80% of use) and glides (17.3%) over the study period (Fig. 6). While they exhibited a high frequency of use of similar habitats, *A. marmorata* and *A. bengalensis* used habitats significantly differently for the whole study duration (χ^2, $P < 0.0001$, see summary for statistical results in the Supplementary Information Table S3), for each season (χ^2, $P < 0.0001$ for each season) and by the time of day (χ^2, $P < 0.0001$ for dawn, day, dusk and night).

Significant differences in seasonal use of different habitats were observed for all eel species (χ^2, $P < 0.0001$ for both species). Both *A. bengalensis* and *A. marmorata* used pools more in winter (73% and 38% of use respectively), spring (59% and 57% respectively), and glides more in summer (49% and 40% respectively) and autumn (39% and 42% respectively). *Anguilla bengalensis* used a wider range of habitats in autumn, while *A. marmorata* used all available habitats through summer and autumn. *Anguilla mossambica* was highly associated with pool habitat (100% in spring and winter) and showed more variability in summer and autumn with the use of glides and runs.

Glides were preferred in spring ($E_1 = 0.4$), summer ($E_1 = 0.6$) and autumn ($E_1 = 0.5$) by *A. bengalensis* (Fig. 6). This species avoided still marginal habitat all year round ($E_1 = -1$). *Anguilla marmorata* did not show clear positive selectivity in spring ($E_1 < 0.1$ for all habitats). In summer, this species preferred glides ($E_1 = 0.5$) and runs ($E_1 = 0.4$) and, in autumn glides ($E_1 = 0.5$), riffles ($E_1 = 0.5$) and still marginal areas ($E_1 = 0.5$) (Fig. 6). *Anguilla marmorata* avoided still marginal areas in spring and winter ($E_1 = -1$) (Fig. 6). While this species had a higher use of pools in winter, it also preferred rapids ($E_1 = 0.5$) and riffles ($E_1 = 0.4$) (Fig. 6).

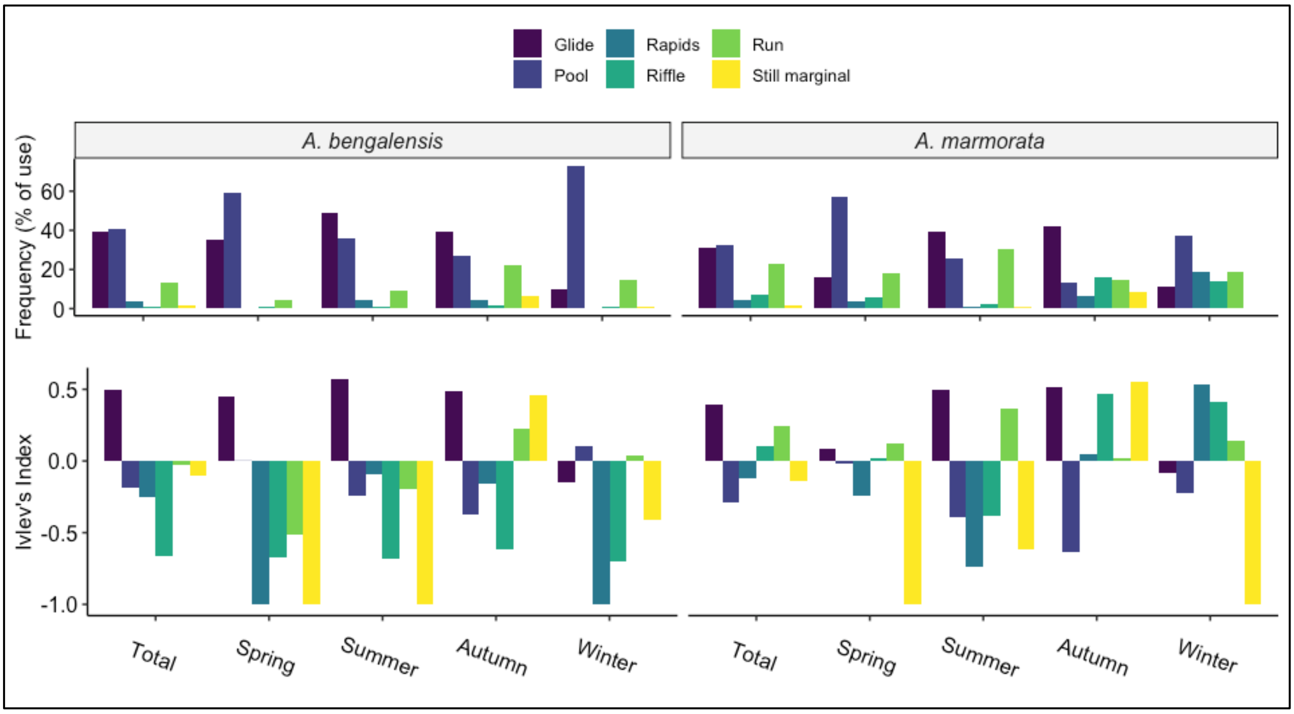

Fig. 6 Seasonal frequency of use of different flow type mesohabitats and Ivlev's selection index for these by three eel species in the Thukela River, South Africa

Discussion

Our study is the first study to have measured the home range and quantified habitat use of freshwater eels in African freshwater habitats. We observed seasonal change in home range, core area and habitat use. In winter, tagged eels exhibited seemingly little activity as suggested by small home range size during that season. We also observed an apparent lack of territoriality as tagged eels shared large portions of their home range and core area both at inter- and intra-specific levels. Tagged eel species used a broad range of mesohabitats, especially glides, but habitat preference changed across seasons, and between species.

We acknowledge the preliminary aspects of our results because of the low sample size, due to the low abundance of the study species at the study site. However, we stress that African eels are no longer abundant and that they are experiencing a dramatic decline in their range distribution in KwaZulu-Natal Province, South Africa (Pike et al., 2019). The abundance of the three eel species at Zingela was greater than at most other sites in KwaZulu-Natal Province, surveyed by similar means by the lead author during 2017-2019 (Hanzen, 2020). The relatively small sample size is a common issue when studying vertebrates of conservation concern, but telemetry does offer a powerful method of collecting a large amount of relevant ecological data per individual in such cases (Cooke et al., 2012). The large number of 'fixes' stratified over diel and seasonal scales are ideal for measuring home range (Cooke et al., 2012) by comparison to capture-mark-recapture methods where a paucity of 'fixes' from recaptures results in a relatively coarse spatio-temporal grain of location records and can introduce inherent bias in space-use estimation (Lucas & Baras, 2000). Nevertheless, capture-mark-recapture, mostly with few recaptures per individual, has been employed for eel 'home range' studies (e.g. Herrera et al., 2019). The tracking period was relatively long for most individuals in the present study, with moderate or large numbers of fixes stratified over diel cycles and seasons, offering high-quality data for home range estimation. The three species studied exhibited high individual variability in sizes of both home ranges and core areas, with very low activities in winter for all species. A lack of apparent territoriality at both inter- and intraspecific levels was observed, translating to spatial and temporal niche partitioning, with use and selection of different mesohabitats.

As riverine resident freshwater eels are globally considered to use very restricted habitat patches, our study's median home range size exceeded our expectations, although it is evident that home range size has been observed to vary widely across studies for north temperate eel species and attributed partly to habitat differences between studies (Herrera et al., 2019). Other species, such as *A. dieffenbachii* and *A. australis* (Jellyman & Sykes, 2003) in New Zealand streams, exhibited restricted longitudinal home ranges of up to 10 m and 30 m, respectively. Ovidio *et al.* (2013) observed home ranges of between 33 and 341 m for European yellow eels. Here, much larger longitudinal home ranges were observed and averaged between 500 and 900 m depending on the species. Barry et al. (2016) is the only study that has used kernel density estimates to calculate home ranges for other eel species. They found lake-dwelling *A. anguilla* 95%-ile home ranges averaged 0.296 km^2 for the broad-headed morphotype and 0.143 km^2 for the narrow-headed morphotype over the northern summer. This is an order of magnitude greater than in the present study (mean 90%-ile home range for the study duration, *A. bengalensis* 0.013 km^2, *A. marmorata* 0.015 km^2 *A. mossambica* 0.029 km^2). Excursive movements were recorded in this study, but long-distance movements are not rare for yellow eel stages and can be observed for other species, such as American eel *A. rostrata,* especially for individuals visiting brackish waters (Béguer-Pon et al., 2015). Given the apparent variability in home range size for European and American eel between habitats, this might also occur for the yellow eel phase of the species studied here; therefore, we recommend further study across a range of habitat types occupied to determine whether this is the case.

In the present study, the home range was lowest in winter for all eel species, and some individuals were located at the same exact position for weeks at a time. Winter dormancy in temperate climates has been observed for European eel (Westerberg & Sjöberg, 2015), as well as for Japanese eel *A. japonica* (Itakura et al., 2018) and American eel *A. rostrata (*Tomie et al., 2017). Butler and Marshal (1996) mentioned minimal activity for *A. bengalensis* during the austral winter, but little is known otherwise. Based on this combined evidence, we recommend not carrying out fyke netting for surveying abundance and distribution of eels in South Africa during austral winters.

Freshwater eels are regarded as habitat generalists (Daverat et al., 2006). In the present study, tagged eels were observed in all available river habitats typical of the lower foothill geomorphological zone (Kleynhans et al., 2005), including deep pools and fast-flowing shallow habitats. In KwaZulu-Natal, as the four tropical African eel species occur in sympatry, different mesohabitat selection may be expected. For instance, in the Indian Ocean Islands, *A.*

mossambica and *A. marmorata* are generally associated with fast-flowing areas of rivers (Valade et al., 2018). Although there was substantial overlap in habitat use between species in this study, *A. bengalensis* showed a consistent preference for glides in spring, summer and autumn, whereas *A. marmorata* preferred a wider range of habitat types across seasons, especially in winter when rapids, runs and riffles were positively selected. Mesohabitat preference might also vary with size, with larger eels known to occupy deeper habitat (Butler & Marshall, 1996; Valade et al., 2018), but this was not examined in the present study.

Freshwater eels are generally considered gregarious species (Tesch, 2003). This phenomenon has been observed for all life stages. Even large eels are gregarious, sharing the same cover for *A. australis* (Jellyman & Chisnall, 1999) and up to 15 yellow eels *A. anguilla* eels sharing the same burrows (Tesch, 2003). In our study, all tagged eels shared a portion of their home range, with up to eight individuals. This highlighted the apparent lack of territoriality at both inter- and intraspecific levels for eels in our study area. However, we also noted that the differences in tagged individuals' capture size in the present study were observed to affect the shared home range size negatively. The spatial overlap within a small stretch of the river may have translated into niche partitioning through the use and selection of different biotopes at different times for the tagged eel species.

We identified key mesohabitats important for freshwater eels, with slow-flowing mesohabitats being predominantly used by 42% of all tracked individuals, but with distinct seasonality of mesohabitat use also. Combining data for all eel species and seasons, we also observed the use of all mesohabitats available in the study area, suggesting that a high diversity of habitats might be valuable for eels, especially if there is a need for niche partitioning among species, for which we found some evidence. Maintaining the natural variability of running water mesohabitats should be a key objective for conserving eels and other native fishes in the Thukela and east-flowing South African rivers. This could be achieved through the implementation or maintenance of environmental flows (O’Brien et al., 2018). South Africa has an ambitious *National Water Act* (Act 36 of 1998) that considers the need for an ecological reserve, which is the reserved flow required for the ecosystem's health, including fish ecological requirements. Meeting the ecological reserve for rivers in South Africa is a serious challenge, as water scarcity is exacerbated by recurring droughts and growing demands from different users (O’Brien et al., 2019). Increasingly, maintenance of natural lotic habitats for aquatic species, including flagship migratory species such as freshwater eels, is at risk in KwaZulu-Natal (Rivers-Moore et al., 2011), but also more widely across Africa. In the Thukela, the ecological reserve flow was determined in 2003 (IWR Environmental, 2003), but it is yet to be officially communicated and implemented. In addition, relatively little monitoring (including water quality, flow or ecological monitoring) is being conducted in the Thukela catchment because of a lack of capacity and financial constraints (DWS, 2019). Equally, access to the suitable habitats available in our study area is important for conserving migratory fish species. While only the Umgeni Water Bulk Transfer Weir stands between Zingela and the sea, the efficiency of its fishway is unknown. Although small eels were caught in the present study, they could have accessed the study area before the construction of the weir. Most east-flowing South African rivers hold many more barriers than the Thukela, again unevaluated in terms of the efficacy of upstream and downstream eel passage. Proper evaluation of passage effectiveness must also be a priority in developing a conservation strategy for eels in Africa.

Conclusions

Eels tagged in this study showed (1) restricted home range and core area, (2) seasonality in term of space use, mesohabitat use and mesohabitat selection, as well as (3) a lack of apparent territoriality. Understanding the spatial ecology of freshwater eels in the Thukela is the first step toward a better understanding of the ecological needs of *A. bengalensis*, *A. marmorata* and

A. mossambica to conserve these elusive species and the rivers they occupy. Our data suggest that access to various habitats may be important for day-to-day and seasonal movements, especially for eels occurring in sympatry. This highlights the importance of maintaining the natural variability of habitats as well as ecological connectivity. Considering this, a comparative study in a degraded and rather uniform system would be useful to test the conclusions drawn here. We recommend that future studies investigate these aspects of their ecology in a system where connectivity has been impaired and where habitats are less heterogeneous. We also recommend that a future study increase the sample size of all species studied here, especially *A. mossambica*, tag a wider range of eel sizes using smaller tags, and also investigate outmigration success of silver eels in South African rivers.

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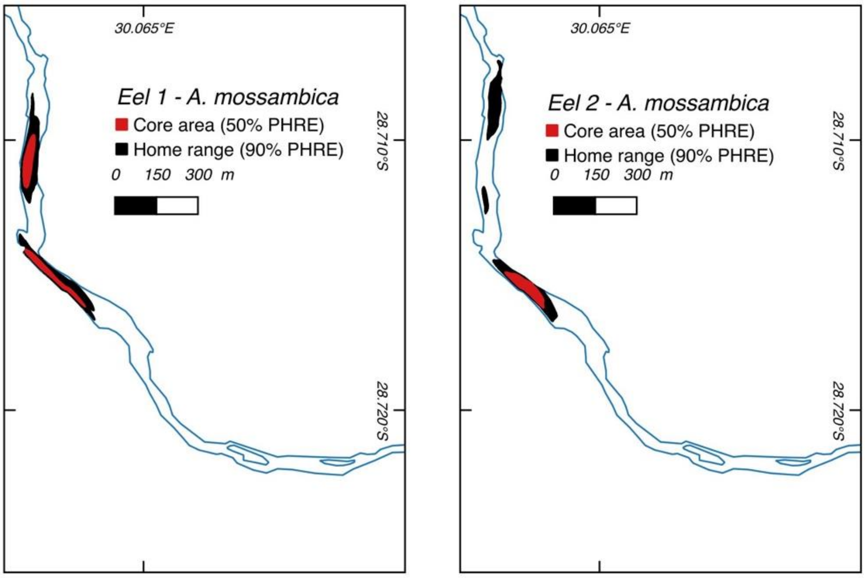
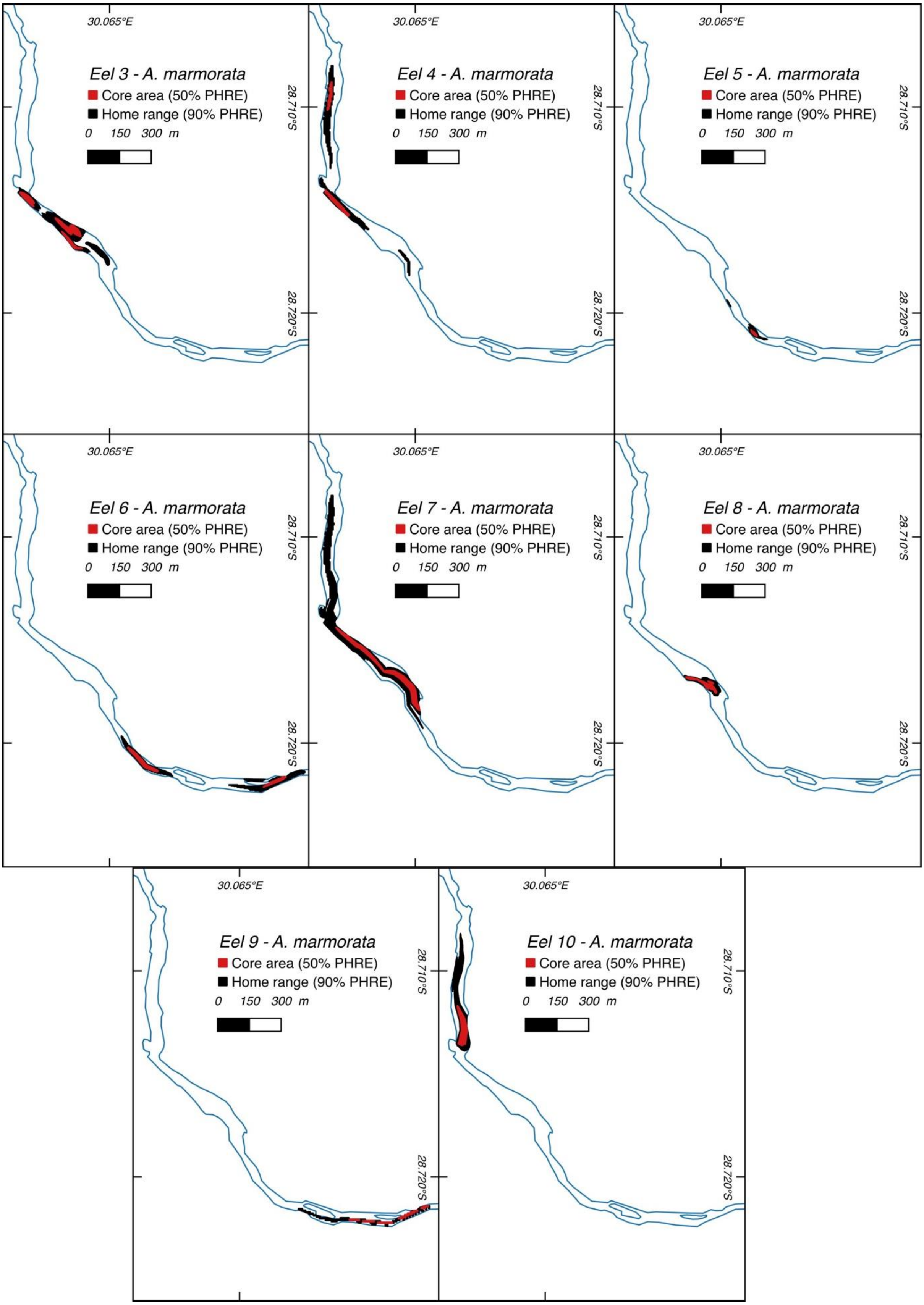
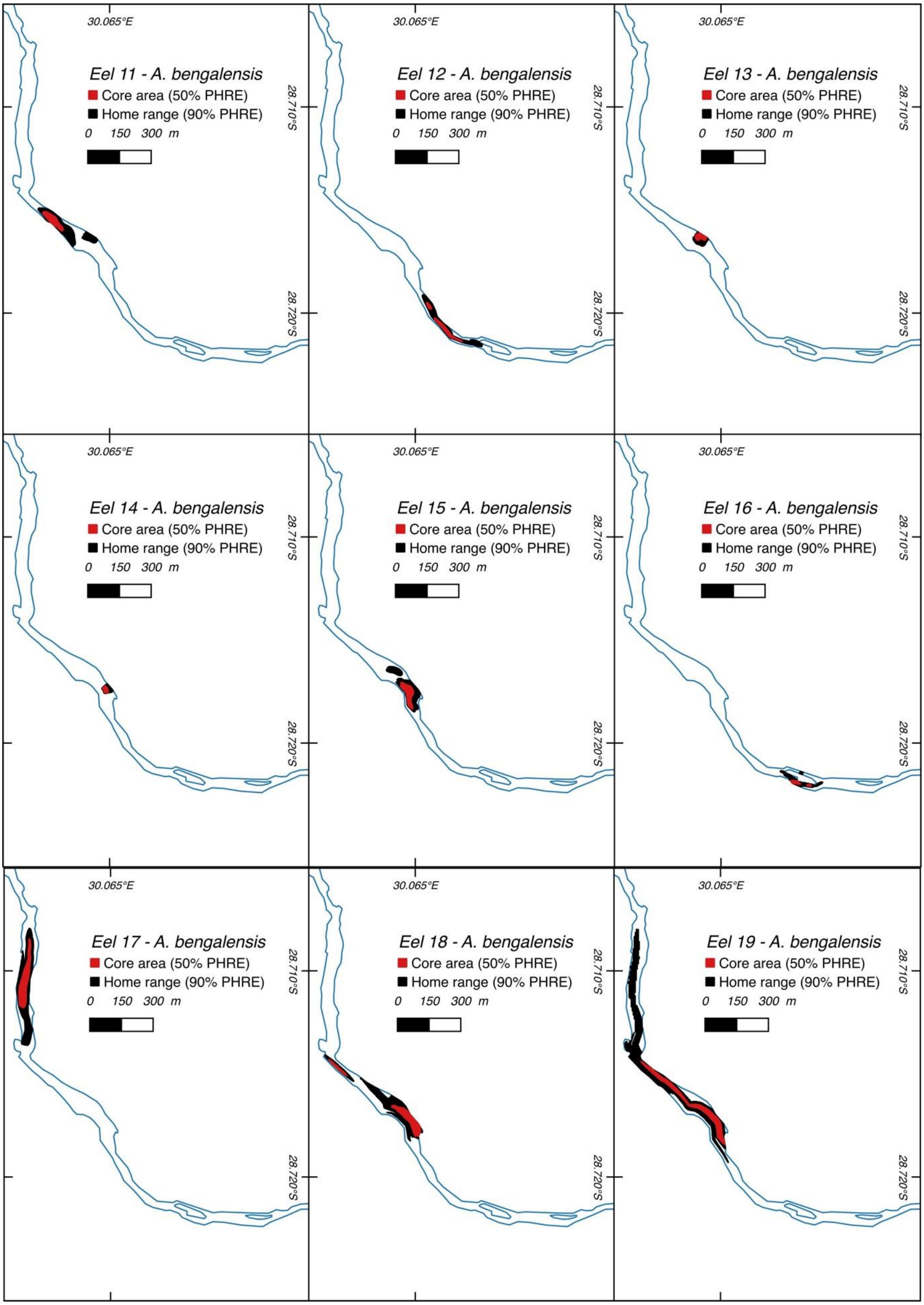
Supplementary information



Supplementary Information Fig. S1. Permissible Home Range Estimation maps for *A. mossambica*, individuals 1 and 2 in the present study.



Supplementary Information Fig. S2 Permissible Home Range Estimation maps for *A. marmorata* individuals 3, 4, 5, 6, 7, 8, 9, and 10 in the present study.



Supplementary Information Fig. S3 Permissible Home Range Estimation maps for *A. bengalensis* individuals 11, 12, 13, 14, 15, 16, 17, 18, and 19 in the present study.

Supplementary Information Table S1. Definitions of the mesohabitats used in the present study.

Mesohabitat	**Definition**
Still marginal	Shallow, water still or eddying, on the margins of the main flow
Pool	Very slow flow or barely perceptible, smooth surface, water flow is silent
Glide	Flow moderate (too fast), smooth surface, water flow is silent
Run	Fast flow, unbroken standing waves at the surface, water flow is silent
Riffle	Fast flow, broken stand-in waves a surface, water flow is audible
Rapids	Very fast, chaotic and turbulent flow, water flow is noisy

Supplementary Information Table S2. The number of tracking events per period of the day and moon phases in the present study.

Period	**New Moon (n)**	**Waning crescent (n)**	**Last Quarter (n)**	**Waning Gibbous (n)**	**Full Moon (n)**	**Waxing Gibbous (n)**	**First Quarter (n)**	**Waxing Crescent (n)**	**Total**
Dawn	50	17	18	32	51	35	54	20	277
Day	61	65	91	93	153	129	63	103	758
Dusk	58	29	46	73	104	81	63	31	485
Night	34	10	17	21	39	46	31	34	232
Total	**203**	**121**	**172**	**219**	**347**	**291**	**211**	**188**	**1752**

Supplementary Information Table S3. Statistical results for home range and core area size and seasonality, habitat use and seasonality in the present study

Kruskall-Wallis	χ^2	**df**	***P***
A. bengalensis			
Seasonal difference in Core area	10.893	3	0.01
Season difference in Home range	7.119	3	0.06
Seasonal difference in Habitat use			
A. marmorata			
Seasonal difference in Core area	8.652	3	0.03
Season difference in Home range	8.919	3	0.03

U-Mann Whitney	***W***	***P***
Differences in area between species		
Home range	32	0.7
Core area	32	0.8
Differences in area within species		
***A. bengalensis* home range**		
Winter vs summer	45	0.03
Winter vs autumn	46	0.02
Winter vs spring	24	0.12
***A. bengalensis* core area**		
Winter vs summer	42	0.006
Winter vs autumn	43	0.003
Winter vs spring	25	0.007
***A. marmorata* home range**		
Winter vs summer	41	0.014
Winter vs autumn	33	0.022
Winter vs spring	33	0.015
***A. marmorata* core area**		
Winter vs summer	37	0.02
Winter vs autumn	37	0.02
Winter vs spring	34	0.008
Overlap intraspecific vs interspecific		
A. bengalensis core	149	0.575
A. bengalensis home range	531	0.974
A. marmorata core	67	0.059
A. marmorata home range	285	0.91

Chi^2	χ^2	***p***
Seasonality in habitat use		
A. bengalensis	138.44	< 0.0001
A. marmorata	235.54	< 0.0001

Differences in habitat use between species			
For the duration of the study		69.053	< 0.0001
For each season			
	Spring	64.23	< 0.0001
	Summer	93.56	< 0.0001
	Autumn	100.6	< 0.0001
	Winter	71.87	< 0.0001
For each season			
	Dawn	47.95	< 0.0001
	Day	86.79	< 0.0001
	Dusk	75.348	< 0.0001
	Night	33.987	< 0.0001

Supplementary Information Table S4. Drivers influencing the size of home range of tagged *A. bengalensis*. (Results from GLMs including SD, 95% confidence interval, *P*-values for all parameter estimates).

Covariates	Estimate	SD	95% confidence		***P* values**
			Lower	**Upper**	
Kg	5.87	2.607	0.76	10.98	0.03*
Season					
Spring	7495.37	6267.998	-4789.68	19780.42	0.24
Summer	6051.15	5747.506	-5213.75	17316.06	0.30
Winter	1399.05	3376.298	-5218.37	8016.48	0.68
Interaction					
Kg:Spring	-4.88	3.424	-11.59	1.83	0.17
Kg:Summer	-3.73	3.299	-10.20	2.74	0.17
Kg:Winter	-4.19	3.299	-9.49	1.10	0.13

Supplementary Information Table S5. Drivers influencing the home range overlap of tagged *A. bengalensis* and *A. marmorata*. (Results from GLMs including SD, 95% confidence interval, *P*-values for all parameter estimates).

Species	**Covariates**	**Estimate**	**SD**	**95% confidence**		***P* values**
				Lower	**Upper**	
A. bengalensis	Ai	0.2	0.04	0.12	0.28	<0.0001***
	Capture	-4.46	1.93	-8.24	-0.67	0.02*
A. marmorata	Ai	0.26	0.08	0.09	0.43	0.004**
	Capture	-1.29	2.87	-6.93	4.34	0.65

P-values 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1