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Population recovery, seasonal site fidelity and daily activity of pirarucu (*Arapaima* spp.) in an Amazonian floodplain mosaic

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Summary

1. Pirarucu (*Arapaima* spp.) are the world's largest scaled freshwater fish, reaching three meters in length and more than 200 kg in weight. Historical overfishing decimated populations of this remarkable fish across Amazonian floodplains, but community-based management programs are now stimulating the recovery of wild populations.

2. Pirarucu evolved a unique set of life history traits, some of which have important implications for population management. Individuals exhibit lateral annual migration patterns during the prolonged annual flood pulse, entering flooded forests to reproduce and forage. During this period, although managed fish stocks become less monopolizable by local communities responsible for managing protected lakes, pirarucu can occupy and reproduce in new environments and thus potentially contribute to population recovery.

3. Here we show a strong pattern of pirarucu (*Arapaima* cf. *gigas*) population recovery under community-based management (CBM) in an area along the Juruá River, in western Brazilian Amazonia. We show evidence of population recovery even outside formal Protected Areas (PAs), reinforcing the suitability of pirarucu CBM as a powerful tool for both biodiversity conservation and the improvement of local livelihoods. We also show pirarucu movements across a floodplain mosaic — including lakes, the main river channel, tributary streams and flooded forests — during the wet season.

4. Our results support evidence of site fidelity among migrating pirarucu, justifying the high effort invested by local communities in seasonally protecting lakes from poachers and illegal fishers. Finally, restricted daily movement patterns by pirarucu support the suitability of population estimates based on day-time counts because the chance of double counting is substantially reduced during the day when these counts are conducted. We highlight the strong suitability of this species for community-based management, since they can (i) replenish new environments during the wet season, through migration and possibly also reproduction, and (ii) be efficiently harvested during the dry season, delivering social and ecological benefits at large spatial scales.

5. Positive examples of fisheries management, which align biodiversity conservation and social development, are important for building optimism, and influencing local and international stakeholders. Our study shows how engaging and empowering local communities to help monitor the movement ecology of target species can be an effective strategy to support the sustainable management of aquatic resources in tropical environments.

Introduction

The pirarucu or giant arapaima (*Arapaima* spp.) is the world's largest scaled freshwater fish, reaching up to three meters in length and more than 200 kg in weight (Nelson, 1994). These fish are an iconic element of Amazonian culture and yet, due to intense exploitation pressure since pre-Columbian times (Prestes-Carneiro *et al.*, 2016), pirarucu populations have suffered dramatic declines, and they have been extirpated in many localities (Castello *et al.*, 2015). To address this, a collaborative community-based management program was developed in several areas across Amazonia over the last 15 years, precluding overexploitation and promoting socially responsible recovery of wild populations (Castello *et al.*, 2009; Campos-Silva & Peres, 2016; Petersen *et al.*, 2016). Pirarucu management has grown to represent one of the most impressive examples of 'win-win' conservation in the Amazon, combining biodiversity conservation with improvements for local welfare (Campos-Silva & Peres, 2016; Campos-Silva *et al.*, 2017).

Pirarucu are highly adapted to Amazonian floodplains, a double-phased aquatic/terrestrial landscape showing marked seasonality, high habitat heterogeneity and an impressive inundation regime, which drives the biological dynamics between alternate dry and wet seasons (Junk, Bayley & Sparks, 1989). The water level oscillation induces stark changes in the landscape, flooding extensive terrestrial habitats, modifying aquatic habitat availability, creating seasonal refuges, connecting populations and influencing the accessibility and impact of commercial fisheries (Junk *et al.*, 1989). As a result, the flood pulse clearly affects fish behaviour and ecology in multiple ways, with subsequent effects on fisheries yields (Fernandes, 1997; Castello, Isaac & Thapa, 2015; Endo, Peres & Haugaasen, 2016). Pirarucu have been used as a model taxon to elucidate fish responses to the prolonged flood pulse phenomenon (Castello, 2008; Araripe *et al.*, 2013). However, our understanding of the role that the annual flood pulse plays in determining fish behaviour remains limited due to practical difficulties in conducting empirical studies in seasonally-flooded forests.

The movement ecology of pirarucu and many other fish populations can be a critical issue in informing their conservation planning. Although considered a 'sedentary' species (Araripe *et al.*, 2013; Núñez-Rodríguez *et al.*, 2015; Watson, Stewart & Kretzer, 2016), pirarucu are known to conduct lateral migrations from lakes to the flooded forests during the wet season, for feeding and reproduction (Castello, 2008; Araripe *et al.*, 2013). These movement patterns can play a critical role in two pathways within community-based management schemes. Firstly, migrant individuals can boost colonization rates of neighbouring lakes through source-sink dynamics (Erickson *et al.*, 2018), increasing the economic value of Protected Area (PA) mosaics, if neighbouring villages in unprotected landscapes also benefit from lake protection. Replenishing wider stocks and delivering important social outcomes for disenfranchised communities makes this a powerful conservation tool, particularly when applied outside PAs (Campos-Silva & Peres, 2016). Secondly, during the wet season, pirarucu stocks cannot be monopolized because migrant individuals are free to move across vast tracts of flooded forest, crossing PA boundaries and occupying a broad range of environments (Castello, 2008), increasing the vulnerability of stocks facing illegal fisheries (Cavole, Arantes & Castello, 2015). In this context, site fidelity becomes an important consideration for villages conducting lake protection, as such effort to protect stocks would clearly only be worthwhile if wide-ranging fish protected during a dry season returned to the same sites in the subsequent dry season.

At a finer scale, a better understanding of the daily movements of pirarucu would also help strengthen existing management techniques, e.g. evaluating the suitability of population census methodology. Harvesting quotas are based upon population counts conducted in the preceding year at each managed lake. This procedure involves the participation of trained fishers, who detect air-breathing pirarucu at the lake surface through both visual and acoustic signals (Castello, 2004). During systematic sampling of each lake, each fisher silently covers a non-overlapping lake area ranging from 0.2 to 2.0 ha, depending on local characteristics such as macrophyte cover and lake area, to avoid double-counts. Pirarucu detections are recorded within 20-min intervals, which are synchronized across observers. In large lakes, counts are conducted over multiple intervals, often taking the entire day to complete a full census. Daily movement patterns are therefore particularly useful to quantify daily distances traveled by each individual and evaluate the probability of double-counts during visual surveys.

Here, we assess three important issues that will help strengthen current pirarucu management. Using data collected during 11 years of pirarucu population recovery within a system of protected lakes both inside and outside formal PAs, we (i) evaluate the potential of pirarucu population replenishment outside PAs to deliver ecological and social outcomes for disenfranchised communities. Using two-years of telemetry data, we also (ii) present seasonal movement patterns across a landscape mosaic, including lakes, the main river channel, streams and the flooded forest to examine the degree of site fidelity in protected lakes; and (iii) present daily activity patterns within protected lakes to assess the suitably of current methods for conducting population counts.

Methods

Study area

This study was conducted across a system of protected lakes both inside and outside two sustainable-use PAs (Reserva de Desonvolvimento Sustentável Uacari and Reserva Extrativista do Médio Juruá, which represents 919,882 ha of upland forest and floodplains) along the Juruá River, a large meandering tributary of the Amazon River in western Brazilian Amazonia (Fig. 1). The Juruá River provides a huge amount of inorganic and organic alluvial deposits for the Amazon lowlands (McClain & Naiman, 2008), with its 'white waters' high in suspended sediment load, turbidity and nutrients. Due to its high productivity, the Juruá River is of high importance as a major fish supplier for the Amazon region (Batista & Petrere Jr., 2003).

The floodplain of the Juruá River experiences a characteristic Amazonian flood pulse, with a typical depth up to 7.5 m for up to 230 d per year (Junk *et al.*, 2011). In the Médio Juruá region, the wet and dry seasons closely approximate periods of high (January – June) and low water levels (August – November), respectively (Hawes & Peres, 2016). There are two main types of lakes spread across the dynamic semi-aquatic landscape (Fig. 1): oxbow lakes - formed from meanders on the main river channel (Stølum, 1996); and ria lakes - former deeply incised river systems, usually adjacent to upland forest (Bertani *et al.*, 2015). Both lake types often linked by paranãs (small channels that connect two lakes). The average lake depth is 11.8 (±6.4) and 14.1 (±6.5) meters during the wet season and 4.2 (±3.4) and 6.7 (±3.5) meters during the dry season, for oxbow and ria lakes, respectively.

Fisheries along the Juruá River

Fisheries are spread across all types of environments in the Juruá River. The lake fisheries are organized as 'Fishing Accords' among local communities at sustainable-use reserves, communities outside these reserves, and the Fishermen Cooperative of Carauari (the nearest town). These agreements are based on three categories of lake resource access: (1) **Open-access lakes,** where commercial fisheries are permitted; (2) **Subsistence-use lakes,** where only local communities responsible for guarding that lake can fish for their own subsistence only; and (3) **Protected lakes,** where both commercial and subsistence fishermen are excluded. In this latter category, pirarucu fisheries are however allowed in some lakes only once each year (see full description in Campos-Silva & Peres, 2016).

Population recovery data

We assessed systematic pirarucu count data obtained at 21 protected lakes located inside two contiguous sustainable-use PAs along the Juruá River, that have been sampled at least once each year during the dry season since 2005 (Table S1). This dataset was obtained through a close partnership between government agencies and local associations. To compare the pirarucu population recovery outside formal PAs, we funded the establishment of eight additional protected lakes employing an identical community-based arrangement as that already occurring inside PAs (see Campos-Silva & Peres, 2016). To achieve this, we conducted several meetings with community leaders that were interested in starting a management program, and together selected the lakes to be protected using a participatory approach. Protected lakes exclude both commercial and subsistence fisheries, with a floating wooden house, usually built at the strategic entrance of the lake, to serve as a full-time surveillance station. Annual counts at these eight newly protected lakes commenced in the dry season of 2013 and encompassed a total of four years of protection by the dry season of 2016.

Movement ecology of pirarucu: capture and transmitter instalment

To quantify the movement dynamics of pirarucu we used conventional radio VHF telemetry (Baras & Lagardère, 1995; Lucas & Baras, 2001). The pirarucu management currently classifies individuals as either juveniles (1–1.5 m) or adults (>1.5 m), corresponding to the minimum catch size (Castello, 2004). Together with experienced local fishermen, we successfully tagged 13 juvenile and adult individuals of *Arapaima* cf. *gigas* (six in 2014, seven in 2015) in four different lakes during the dry season, using 100-m wide gill-nets (4 m high, 60 mm mesh size). We focused our sampling on individuals with a maximum of 1.60 m in length, due to their relative ease of capture and presumed resilience compared to large adults. Captured individuals were carefully restrained inside a large wooden canoe using a soft and water-soaked hammock, with their heads covered by a wet towel to reduce stress. Internal tag transmitters (Lotek; 16 mm diameter x 73 mm length, 25 g weight) were implanted in the intra-peritoneal cavity, just above the cloaca, immediately after capture. We removed a few scales as necessary and used a scalpel to make a small incision to insert the transmitter. The opening was then stitched up with surgical thread, cleaned with alcohol, and a scale was stuck over the top with surgical glue to prevent any possible attention from carnivorous piranhas (*Serrasalmus* spp.). Due to the absence of a standard protocol for installing transmitters on pirarucu, we performed dozens of tests on the carcasses of fish killed as part of the regulated annual management harvest, in order to develop a quick, efficient method that minimised transmitter implantation time and potential stress. During the procedure we recorded the standard length and weight of all individuals (Table 1). Immediately after transmitters were fitted, all fish were released in a shallow and quiet place and observed until they showed signs of complete recovery. The total handling time (from capture to release) never exceeded four minutes. In this study only one fish died during the procedures of surgery. This study was authorised by the appropriate Brazilian authorities (ICMBio, permit number 45054-2).

Pirarucu telemetry

Radio tracking started in August 2014 and was performed continuously for two years to map seasonal and daily movement patterns. For seasonal movements, the locations of individual pirarucu were recorded weekly by a trained local resident using a 3-element antenna and a Lotek Biotracker receiver (Lotek Wireless Inc., Newmarket, Ontario, Canada), and recorded with a GPS Garmin unit (Garmin International, Inc., Olathe, KS) with an average accuracy of ±3 m. During the dry season, sampling consisted of a comprehensive scan of selected areas, including lakes and paranãs. The vastly expanded potential search area during the wet (high-water) season meant that, beyond lakes and paranãs, telemetry expeditions into the flooded forest were necessarily restricted to selected areas.

To understand and quantify the foraging behaviour of pirarucu over the diurnal cycle, we conducted a paired sample on the same individuals, for three continuous hours during both diurnal (07:00h - 10:00h) and nocturnal (19:00h - 22:00h) sessions. Diurnal and nocturnal movements were recorded for eight individuals on 17 days during the 2015 dry season (Table 2), when fish were restricted to lakes and paranãs where they could be easily followed. GPS locations were recorded in each three-hour session at 30-minute intervals.

Ethnoecology

We conducted 40 semi-structured interviews (Bernard, 1994) with 40 highly experienced pirarucu fishermen from 30 communities along a 500 km section of the Juruá River. During interviews, we objectively asked about their overall perception of the types of habitats used by pirarucu, the level of habitat fidelity, and any differences in movement ecology between adults and juveniles. Each interview lasted up to 30 min and was facilitated by the long-term experience of fishermen in terms of their frequent observational exposure to pirarucu populations at community lakes. All selected interviewees boasted more than 20 years of experience of pirarucu harvesting.

Data analysis

To understand the potential population recovery outside formal PAs, we conducted systematic pirarucu counts (*sensu* Castello, 2004) in protected lakes both inside and outside PAs. We then estimated the total population growth rates (G_N) and annual population growth rates (Ann. G_N) by calculating changes in pirarucu population sizes between the first to the last year (including both adults and juveniles): $G_N = \left(\frac{yn - y1}{y1}\right)$ and $Ann.G_N = (yn/y1)^{\frac{1}{Nyears}} - 1$. Single-case statistical analyses with Kruskal-Wallis nonparametric tests were performed to test for differences in total growth rates between protected lakes inside and outside PAs.

We plotted all recorded fish locations in ArcGIS 10.3 (http://www.esri.com) to produce movement maps of tracked individuals and used paired t-tests to compare the average and total travel distances during day and night periods. All statistical analyses were conducted in R 3.3.2 (R Development Core Team, 2015).

Results

Rates of population recovery within and outside sustainable-use protected areas

Rates of population recovery were highly positive for protected lakes, both inside and outside formal PAs (Fig. 2). A reduction in the population size of pirarucu was observed in only a single protected lake (Table S1). Protected lakes hosted an average of 505 pirarucu individuals (range = 50 – 2,878) inside PAs, compared to 389 individuals (range = 142 – 1,354) outside PAs. Over 11 years of lake protection, pirarucu populations inside PAs experienced annual growth rates ranging from -4.1 to 1129.9% (mean = 76%, n= 21, $Ann.GN$ estimates). After four years of equivalent protection in lakes outside formal PAs, the mean population recovery was 39%, ranging from 16.5 % to 112.8 % ($N = 8$, $Ann.G_N$ estimates). Considering the first and last years of management at each protected lake, population sizes increased by 425.2% on average inside PAs, ranging from -19.3 % to 2,917.5 % (mean interval = 6.3 ± 2.01 yrs, N = 21) and 397.5% outside PAs, ranging from 84.4 % to 1,950 % (4 yrs, $N = 8$). In exceptional cases, pirarucu stocks increased up to 30- and 20-fold inside and outside PAs, respectively. There were no differences in pirarucu population growth rates between protected lakes inside sustainable-use PAs and those under strict fishing agreements outside reserves (Kruskal-Wallis test, $\chi^2 = 0.03$, 2 df, p = 0.8). All recovery estimates are available in Table S1.

Seasonal movements

We conducted 87 days of positional sampling, yielding a total of 522 hours of active search time and 309 GPS positional records (125 dry season; 184 wet season) from target individuals over the two years. Our results confirm that pirarucu depart from lakes where they are resident throughout the dry season, often travelling thereafter many kilometres in the flooded forest, passing through lakes, *paranãs*, streams, and the main river channel (Figure 3). We highlight an interesting case where one individual (Juliana), captured and tagged in a protected lake within a PA, travelled at least 30 km, through two PAs before eventually being killed by a fisherman outside the PA boundary (Figure 4). This movement was made during the period of rising water levels, and therefore the flooded forest was not entirely available for pirarucu movements. We identified a probable route between the recorded positional points, based on features of landscape, and local knowledge (Figure 4).

Although pirarucu potentially dispersed out of protected lakes during the wet season, 83% of our tracked individuals returned in the following year to the same protected lake, in which they had been tagged for the first time. Impressively, half of all individuals captured in the first year returned to the same lakes for two consecutive years. For those animals captured in the second year, six of seven marked individuals returned to the same lake prior to the following dry season (Table 1).

Daily movements

During the dry season, the movement ecology of pirarucu is restricted to protected lakes, which become discrete units in the floodplain landscape. We found that pirarucu are more active at night than during the day (Figure 5). This result was consistent in terms of both mean (night = 155.9 ± 96.6 m; day = 39.7 ± 98.1 m; $t = -4.80$, $df = 16$, $p = 0.0001$) and maximum travel distances moved in 3 hour periods (night = 509.2 ± 343.4 m; day = 140.01 ± 345.0 m; $t = -4.25$, $df = 16$, $p = 0.0006$).

Ethnoecological knowledge

Of the 40 interviewed fishermen, 22 reported that juveniles typically migrate in groups during the wet season, leaving the lakes for a broad range of environments. Of those 40 fishermen, 35 reported that pirarucu are sensitive to noise pollution (e.g. from outboard motors) and are only to be found in quiet places. All interviewees reported that adults build their nests in shallow places within flooded forests at the beginning of the rainy season, when floodwater levels first begin to rise. After the fry hatch, adult males become sedentary and are responsible for highly targeted parental care, remaining nearby for approximately three months without any major displacements. Local fishermen also confirm our finding that pirarucu are more active during the night, mainly between dusk (18:00h) and midnight (00:00h), when individuals show an intense activity peak, mainly due to foraging behaviour.

Discussion

Population recovery

Our results reinforce the suitability of pirarucu management to be incorporated into the broad range of governance systems currently applied within Amazon floodplains. The population recovery rates recorded (e.g. Campos-Silva & Peres, 2016) suggest that pirarucu populations show high resilience to past over-exploitation and can rapidly replenish depleted environments. The astonishing population growth in community-protected lakes, both inside and outside formal PAs, can boost the conservation of this historically overexploited species, delivering important socioeconomic outcomes and aligning environmental and social aspirations. Multiple mechanism are likely responsible for the rapid recovery of pirarucu populations, but our findings provide important insights.

Seasonal migration

Our results support evidence for the recurrent use of flooded forest during the lateral migration of pirarucu (Castello, 2008; Araripe *et al.*, 2013; Hermann *et al.* 2016). Fish movement patterns, at a local scale, can be explained by both abiotic conditions and resource availability (Winemiller & Jepsen, 1998). For pirarucu, lateral migration provides a source of high quality food, since the flooded forest supports both the main fish prey of adults, such as detritivorous and omnivorous fish species (Castello, 2008; Carvalho *et al.*, 2018), and the insects, fish larvae, and other small organisms which constitute the bulk of the fingerling diet (Junk *et al.*, 1989; Queiroz, 2000; Carvalho *et al.*, 2018). Calm sheltered shallows within the flooded forests also provide the preferred nesting sites for adults to spawn.

Entering the flooded forest in search of nesting sites and food resources during the wet season plays a crucial ecological role, in terms of parental care and reproductive success. In addition, the seasonal migration behaviour displayed by pirarucu makes them a model species predisposed for sustainable harvesting. During the dry season, movements are highly restricted, and pirarucu stocks are therefore easily monopolized and guarded as a resource that can be effectively monitored and efficiently exploited according to management rules. In contrast, widely scattered pirarucu populations cannot be monopolized during the wet season, and individuals freely move beyond the confines of protected lakes, increasing the probability of replenishing stocks in neighbouring unprotected lakes by producing young that subsequently disperse. Migration patterns during the flood pulse also show a spillover effect that extend the benefits of lake protection to people living far from protected lakes. This was exemplified by one individual, which was originally marked within a protected lake, but subsequently travelled more than 30 km, passing through boundaries of two large PAs before being harvested outside the PAs. This movement behaviour during the flood pulse enables the occurrence of pirarucu in unprotected regions, contributing to both (i) the potential establishment of new populations in surrounding aquatic environments and (ii) the food security of marginalised communities without access to a protected lake. This is especially important considering the high subsistence, cultural and commercial value of pirarucu (Veríssimo, 1895; Campos-Silva & Peres, 2016).

Despite the identified potential of population spillover, we show that pirarucu exhibit a substantial degree of supra-annual site fidelity. The high proportion of individuals that return annually to the same protected lake after each flood event is beneficial to justify the high effort of lake protection and consequently sustain long-term community participation and compliance. Local fishers protect their lakes 24-hours a day as the flood waters recede (from approx. May to July) and then throughout the subsequent dry season (until approx. December). Protected lakes effectively function as high-interest savings accounts, ensuring substantial revenues per family household, and improving local welfare (Campos-Silva & Peres, 2016), but the high investment in protection, in terms of cost and effort, would not be viable if the pirarucu population dispersed randomly across the floodplain landscape during each flood pulse and failed to return in the subsequent dry season.

Studies elsewhere in Amazonia to date suggest that pirarucu populations have a high level of genetic admixture at a local scales due to lateral migration, reproductive traits and dispersal patterns of adults and juveniles (Araripe *et al.*, 2013; Watson *et al.*, 2016). If individuals returned randomly to multiple lakes following each flood event, this would contribute to a lower genetic diversity (Araripe *et al.*, 2013). However, our results show that these return movements are not random in a protected and unprotected lake mosaic where individuals make choices about the suitability of different lakes. Reports from experienced local fishermen introduce an interesting untested hypothesis that after the floodwaters recede, pirarucu remain only in protected lakes, using anthropogenic noise levels as a cue to determine lake protection status. This behaviour can be associated with the so-called 'landscape of fear', where animal movements are shaped by predation risk (Laundré, Hernández & Altendorf, 2001; Laundré *et al.*, 2010). In fact, the ecology of fear has been recognized as fundamental in understanding predator-prey dynamics and their ecosystem-wide consequences (Estes *et al.*, 2011; Gallagher *et al.*, 2017), but rarely in the context of aquatic vertebrates.

Group migration hypothesis

Based on the testimony of local fishermen recorded through our ethnoecological approach, we suggest that groups of juvenile pirarucu likely conduct gregarious migration events during the floodwater season. While water levels are high they are able to travel through the flooded forest, exploring the wide range of food items available, but as water levels recede, the groups apparently use the soundscape of each lake to select their preferred dry season refuge, as already demonstrated for other fish species (Scholik & Yan, 2001). This behaviour would help explain the large population growth observed in protected lakes year on year, which is unlikely to be maintained by reproduction and internal recruitment alone. In our study area, for instance, the pirarucu population within protected lakes has been recorded to increase 31-fold in a single year. This poorly documented group migration phenomenon could also help explain the marked genetic homogeneity observed at such a small scale (Araripe *et al.*, 2013).

Daily movements: reinforcing the suitability of counting methodology

The method for conducting pirarucu counts is now well established and shows a strong correlation with mark-recapture population estimates (Castello, 2004). After sunrise, fishers count juveniles and adults breaking the surface within 20-min intervals. Depending on the lake area, these counts can be repeated to cover the entire lake area. Our results provide further documented support for the feasibility of these methods, because pirarucu are relatively sedentary during the first hours after dawn, reducing the chance of those individuals being double counted. The higher movement rates during night-time also justify the frequent local preference to conduct nocturnal fishing trips during the harvest period. This is also supported by widespread reports from fishers that catch rates are higher at night than during the day, despite the consistent use of gill-nets as the only fishing method.

Implications for community-based management

Our study presents new insights on the movement ecology of pirarucu and the high suitability of this species for a highly promising community-based management arrangement. The preliminary data presented here are only a first step towards understanding the nuances of pirarucu migration. It is important to quantify the movement patterns of large-bodied fish in

Amazonian floodplains, including home range configuration and dispersal capacity, , to better inform the sustainable management of subsistence and commercial fisheries. Conventional telemetry estimates can severely underestimate distances travelled by Amazonian fish in floodplain environments due to the practical difficulties of such work in vast areas of flooded forest where accessibility and mobility are reduced for observers during the high-water period. We therefore suggest that GPS or ultrasonic telemetry options may be useful, particularly during the high-water season, to more accurately understand local and landscape-scale fish migration patterns in Amazonian floodplains. Higher-resolution pirarucu movement data during both the high- and low-water seasons would help design an effective spatially explicit demographic model that can optimize the spatial structure of protected and unprotected floodplain lakes.

Conclusions

The alignment of biodiversity conservation and social welfare aspirations is imperative, particularly in tropical developing countries. Focussing on bright spots can help identify successful strategies and build conservation optimism to influence local and international decision makers and stakeholders (Cvitanovic & Hobday, 2018). We show how empowering local communities through fishing agreements can be a powerful tool to encourage the sustainable management of aquatic resources in tropical floodplains. Our study also highlights the importance of understanding how target species move within the waterscape as daily to seasonal movement patterns may influence the colonization rates of new areas and the motivation of local communities to engage in conservation projects. Studies such as ours, that show conservation gains accompanied by strong social outcomes, provide a positive example for this promising tool to be applied more widely, even outside existing protected areas.

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References

Araripe J., Rêgo P.S. do, Queiroz H., Sampaio I. & Schneider H. (2013) Dispersal capacity and genetic structure of *Arapaima gigas* on different geographic scales using microsatellite markers. *PLoS One* **8**, e54470.

Baras E. & Lagardère J.P. (1995) Fish telemetry in aquaculture: review and perspectives. *Aquaculture International* **3**, 77–102.

Batista V.S. & Petrere Júnior M. (2003) Characterization of the commercial fish production landed at Manaus, Amazonas State, Brazil. *Acta Amazonica* **33**, 53–66.

Bernard H. (1994) *Research Methods in Anthropology: qualitative and quantitative approaches*, 4th edn. Altamira Press, London.

Bertani T.C., Rossetti D.F., Hayakawa E.H. & Cohen M.C.L. (2015) Understanding Amazonian fluvial rias based on a Late Pleistocene-holocene analog. *Earth Surface Processes and Landforms* **40**, 285–292.

Campos-Silva J.V. & Peres C.A. (2016) Community-based management induces rapid recovery of a high-value tropical freshwater fishery. *Scientific Reports* **6**, 34745.

Campos-Silva J.V., Peres C.A., Antunes A.P., Valsecchi J. & Pezzuti J. (2017) Community-based population recovery of overexploited Amazonian wildlife. *Perspectives in Ecology and Conservation* **15**, 266–270.

Carvalho F., Power M., Forsberg B.R., Castello L., Martins E.G. & Freitas C.E.C. (2018) Trophic ecology of Arapaima sp. in a ria lake-river-floodplain transition zone of the Amazon. *Ecology of Freshwater Fish* **27**, 237–246.

Castello L. (2004) A method to count pirarucu *Arapaima gigas*: fishers, assessment, and management. *North American Journal of Fisheries Management* **24**, 379–389.

Castello L. (2008) Lateral migration of *Arapaima gigas* in floodplains of the Amazon. *Ecology of Freshwater Fish* **17**, 38–46.

Castello L., Arantes C.C., Mcgrath D.G., Stewart D.J. & Sousa F.S. de (2015) Understanding fishing-induced extinctions in the Amazon. *Aquatic Conservation: Marine and Freshwater Ecosystems* **25**, 587–598.

Castello L., Isaac V.J. & Thapa R. (2015) Flood pulse effects on multispecies fishery yields in the Lower Amazon. *Royal Society Open Science* **2**, 150299.

Castello L., Viana J.P.J., Watkins G., Pinedo-Vasquez M. & Luzadis V.A. (2009) Lessons from integrating fishers of *Arapaima* in small-scale fisheries management at the Mamirauá Reserve, Amazon. *Environmental Management* **43**, 197–209.

Cavole L.M., Arantes C.C. & Castello L. (2015) How illegal are tropical small-scale fisheries? An estimate for arapaima in the Amazon. *Fisheries Research* **168**, 1–5.

Cvitanovic, C. & Hobday, A. J. (2018) Building optimism at the environmental science-policy-practice interface through the study of bright spots. *Nature Communications*, ***9***, 3466.

Endo W., Peres C.A. & Haugaasen T. (2016) Flood pulse dynamics affects exploitation of both aquatic and terrestrial prey by Amazonian floodplain settlements. *Biological Conservation* **201**, 129–136.

Erickson R.A., Diffendorfer J.E., Norris D.R., Bieri J.A., Earl J.E., Federico P., … Thogmartin, W.E. (2018) Defining and classifying migratory habitats as sources and sinks: the migratory pathway approach. *Journal of Applied Ecology* **55**, 108–117.

Estes J.A., Terborgh J., Brashares J.S.J., Power M.E., Berger J., Bond W.J., … Wardle, D.A. (2011) Trophic downgrading of planet Earth. *Science* **333**, 301–306.

Fernandes C.C. (1997) Lateral migration of fishes in Amazon floodplains. *Ecology of Freshwater Fish* **6**, 36–44.

Gallagher A.J., Creel S., Wilson R.P., & Cooke, S.J. (2017) Energy landscapes and the landscape of fear. *Trends in Ecology & Evolution* **32**, 88–96.

Hawes J.E. & Peres C.A. (2016) Patterns of plant phenology in Amazonian seasonally flooded and unflooded forests. *Biotropica* **48**, 465–475.

Hermann, T.W., Stewart, D.J., Limburg, K.E. & Castello, L. (2016) Unravelling the life history of Amazonian fishes through otolith microchemistry. *Royal Society Open Science* **3**, 160206.

Junk W.J., Bayley P.B. & Sparks R.E. (1989) The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences* **106**, 110–127.

Junk W.J., Piedade M.T.F., Schöngart J., Cohn-Haft M., Adeney J.M. & Wittmann F. (2011) A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands* **31**, 623–640.

Laundré J.W., Hernández L. & Altendorf K.B. (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* **79**, 1401–1409.

Laundré J.W., Hernandez L., Ripple W.J., Laundre J.W., Hernandez L. & Ripple W.J. (2010) The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal* **3**, 1–7.

Lucas M.C. & Baras E. (2001) Migration and spatial behaviour. In: *Migration of Freshwater Fishes*. (Eds M.C. Lucas & E. Baras), pp. 1–13. Blackwell Science Ltd, Oxford.

McClain M.E. & Naiman R.J. (2008) Andean influences on the biogeochemistry and ecology of the Amazon river. *BioScience* **58**, 325–338.

Nelson J.S. (1994) *Fishes of the World*. John Wiley and Sons, Inc, New York.

Núñez-Rodríguez J., Duponchelle F., Cotrina-Doria M., Renno J.F., Chavez-Veintimilla C., Rebaza C., … Baras, E. (2015) Movement patterns and home range of wild and re-stocked *Arapaima gigas* (Schinz, 1822) monitored by radio-telemetry in Lake Imiria, Peru. *Journal of Applied Ichthyology* **31**, 10–18.

Petersen T.A., Brum S.M., Rossoni F., Silveira G.F.V. & Castello L. (2016) Recovery of *Arapaima* sp. populations by community-based management in floodplains of the Purus River, Amazon. *Journal of Fish Biology* **89**, 241–248.

Prestes-Carneiro G., Béarez P., Bailon S., Py-Daniel A.R. & Neves E.G. (2016) Subsistence fishery at Hatahara (750–1230 CE), a pre-Columbian central Amazonian village. *Journal of Archaeological Science: Reports* **8**, 454–462.

Queiroz H. (2000) *Natural history and conservation of pirarucu,* Arapaima gigas*, at the Amazonian Várzea: red giants in muddy waters*. PhD thesis, University of St. Andrews.

R Development Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

Scholik A.R. & Yan H.Y. (2001) Effects of underwater noise on auditory sensitivity of a cyprinid fish. *Hearing Research* **152**, 17–24.

Stølum H.-H. (1996) River meandering as a self-organization process. *Science* **271**, 1710–1713.

Veríssimo J. (1895) *A Pesca na Amazônia*. Livraria Clássica Francisco Alves, Rio de Janeiro.

Watson L.C., Stewart D.J. & Kretzer A.M. (2016) Genetic diversity and population structure of the threatened giant *Arapaima* in southwestern Guyana: implications for their conservation. *Copeia* **104**, 864–872.

Winemiller K.O. & Jepsen D.B (1998) Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology* **53**, 267–296.

Figure legends

Figure 1. Study area along the Juruá River, showing examples of relevant aquatic landscape features within the harvesting mosaic. In A, the yellow polygon shows the study reserve (RDS Uacari) with its neighbouring extractive reserve (RESEX Médio Juruá, orange) and an indigenous territory (TI Deni, purple). Small black and white circles indicate protected lakes inside and outside formal PAs, respectively; red circles represent human settlements. In B, yellow and blue circles indicate capture locations of individual pirarucu in 2014 and 2015, respectively; red circles represent human settlements. This map was generated in ArcGIS 10.3 (http://www.esri.com).

Figure 2. Total pirarucu population growth rates (G_N) in protected lakes inside (blue) and outside (red) formal PAs. Growth estimates did not differ between lakes inside and outside PAs (growth over 11 and 4 years, respectively).

Figure 3. Landscape features used by pirarucu during the dry and wet seasons. Coloured circles indicate each tracked pirarucu individual.

Figure 4. Example of a track from one pirarucu individual (Juliana), which was captured in a protected lake (1). This fish travelled about 30 km across the flooded forest, crossing the boundaries of a sustainable use reserve (RDS Uacari) and an indigenous territory (TI Dení), and was opportunistically caught by a fisherman in the main channel of the Juruá River, in front of a community located outside any PA (2). Yellow circles represent confirmed radio-tracked locations; yellow line is a hypothesised approximate most plausible route created using suitable landscape features; black dashed lines represent PA boundaries.

Figure 5. Effect of the diurnal cycle on pirarucu behavior in terms of total distance travelled (m) by individual pirarucu (N=13) during a three-hour observation session; boxplots and connected points show the paired design, comparing day (yellow) and night (purple) activity samples from the same individuals.

Tables

Table 1. Identity, measurements (TL = Total Length) and site fidelity each dry season (2014-2016) of the 13 *Arapaima* cf. *gigas* individuals tagged and radio tracked in the Médio Juruá, Amazonas, Brazil. Symbols (ł and łł) represent one and two years of detection at the same lake where initially tagged; NA = Not Applicable, ND = Not Detected.

ID	Name	Lake	TL (cm)	Weight (kg)	2014	2015	2016
1	Juliana	Marari Grande	122	18	Tagged	Harvested	NA
2	Macedoni łł	Marari Grande	160	35	Tagged	Detected	Detected
3	Micaele łł	Macaco	125	22	Tagged	Detected	Detected
4	Vernior	Macaco	136	29	Tagged	ND	ND
5	Roana łł	Veado	126	25	Tagged	Detected	Detected
6	Valdir ł	Veado	134	25	Tagged	Detected	Harvested
7	Juliana 2 ł	Marari Grande	151	32	NA	Tagged	Detected
8	Tio Chico ł	Marari	147	28	NA	Tagged	Detected
9	Preto ł	Camponesa	128	22	NA	Tagged	Detected
10	Dona Graca ł	Camponesa	168	41	NA	Tagged	Detected
11	Pracuuba ł	Camponesa	157	39	NA	Tagged	Detected
12	Eder ł	Macaco	134	28	NA	Tagged	Detected
13	Gracia	Macao	159	39	NA	Tagged	ND

Table 2. Eight pirarucu individuals monitored for daily movement activity and sample size per individual (total = 19 days). Each monitoring sample lasted for three consecutive hours during both the day (07:00h - 10:00h) and night (19:00h - 22:00h), recording GPS locations at 30-minute intervals.

ID	**Name**	**Lake**	**Lat.**	**Long.**	**N (days)**
10	Dona Graça	Camponesa	- 5.93763	- 67.7535	2
11	Pracuuba	Camponesa			2
9	Preto	Camponesa			2
2	Macedoni	Marari Grande	-5.94104	-67.7664	2
8	Tio Chico	Marari Grande			2
3	Micaele	Macaco	-5.9775	-67.7673	2
5	Roana	Veado	-5.8269	-67.7987	2
4	Valdir	Veado			3

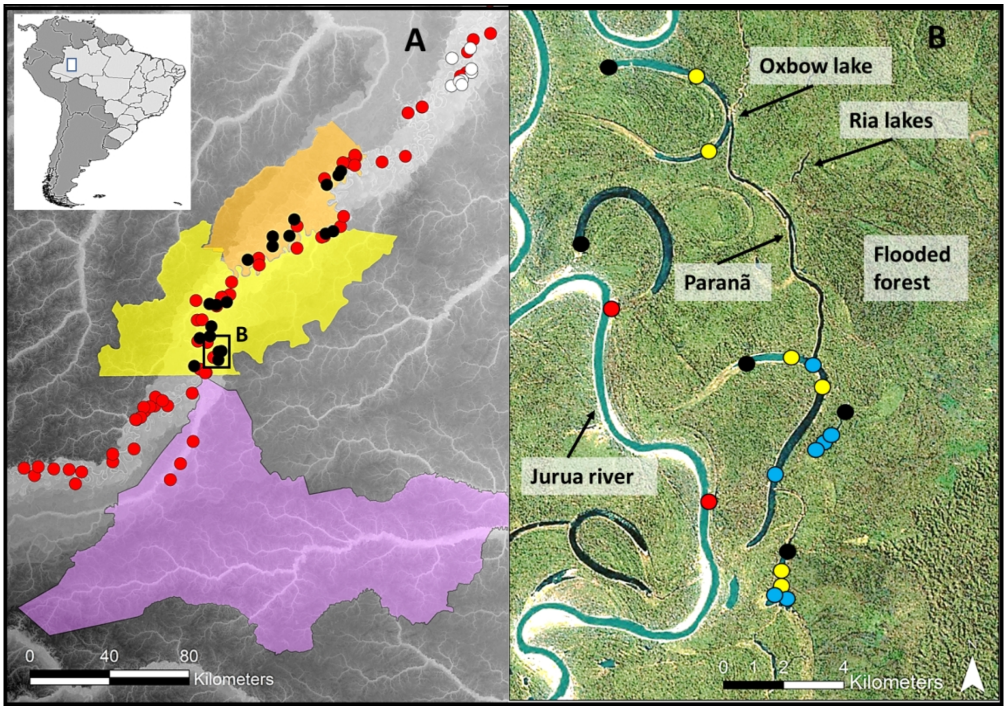

Figure 1. Study area along the Juruá River, showing examples of relevant aquatic landscape features within the harvesting mosaic. In A, the yellow polygon shows the study reserve (RDS Uacari) with its neighbouring extractive reserve (RESEX Médio Juruá, orange) and an indigenous territory (TI Deni, purple). Small black and white circles indicate protected lakes inside and outside formal PAs, respectively; red circles represent human settlements. In B, yellow and blue circles indicate capture locations of individual pirarucu in 2014 and 2015, respectively; red circles represent human settlements. This map was generated in ArcGIS 10.3 (http://www.esri.com).

272x191mm (150 x 150 DPI)

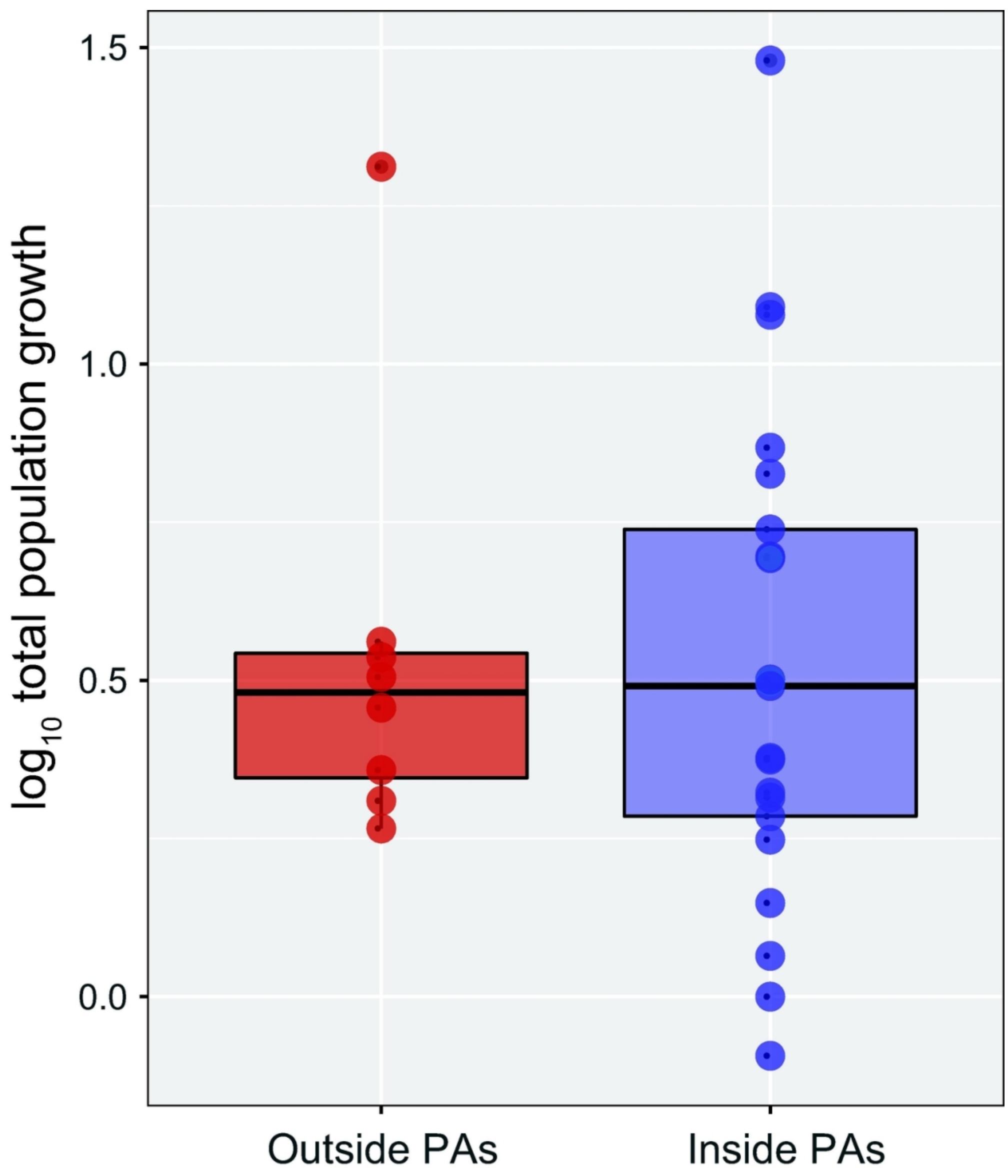

Figure 2. Pirarucu population growth as a function of the number of years of community-based protection in lakes inside (blue) and outside protected areas (red). There was no difference between protected lakes inside and outside PAs.

118x138mm (300 x 300 DPI)

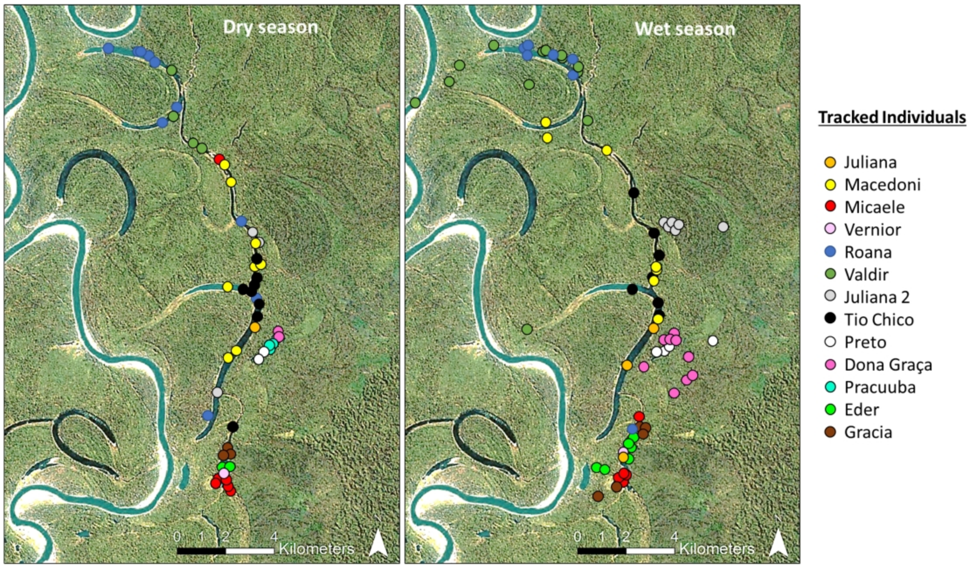

Figure 3. Landscape features used by pirarucu during the dry and wet seasons. Coloured circles indicate each tracked pirarucu individual.

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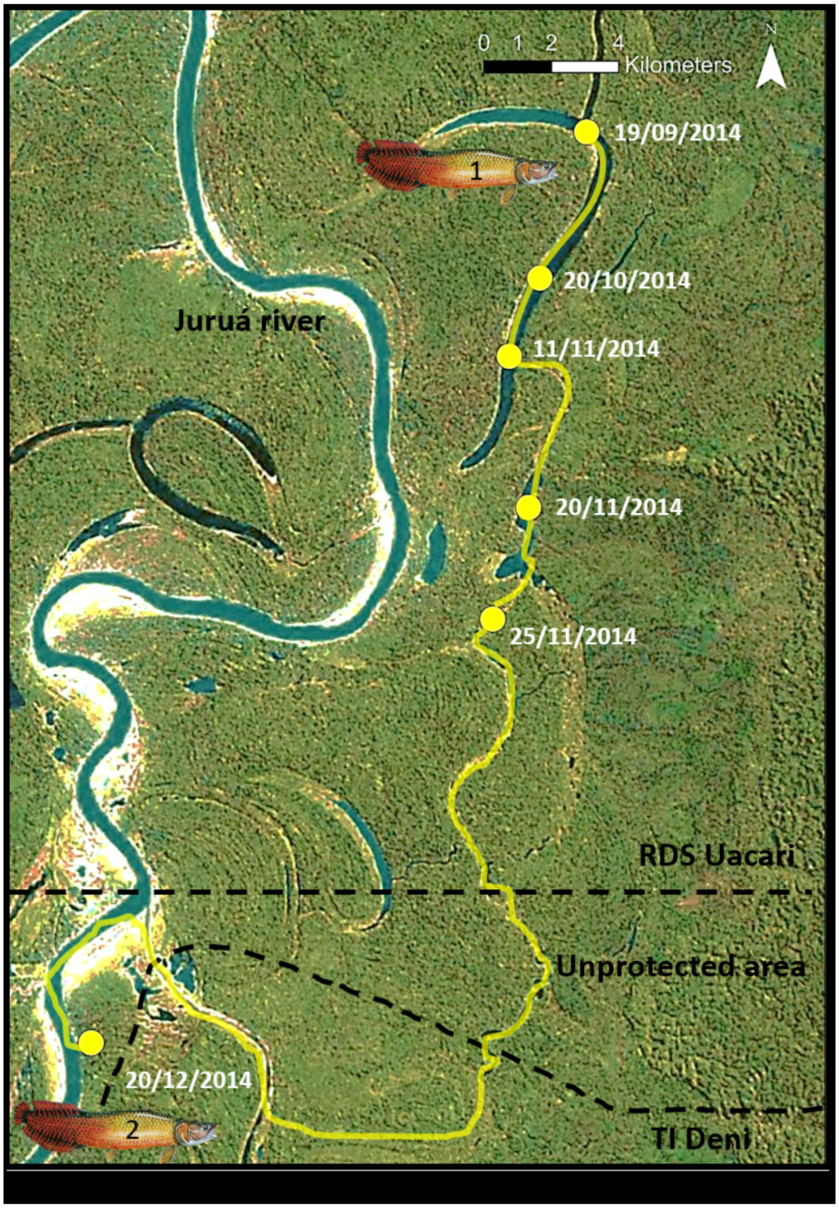

Figure 4. Example of a track from one pirarucu individual (Juliana), which was captured in a protected lake (1). This fish travelled about 30 km across the flooded forest, crossing the boundaries of a sustainable use reserve (RDS Uacari) and an indigenous territory (TI Dení), and was opportunistically caught by a fisherman in the main channel of the Juruá River, in front of a community located outside any PA (2). Yellow circles represent confirmed radio-tracked locations; yellow line is a hypothesised approximate most plausible route created using suitable landscape features; black dashed lines represent PA boundaries.

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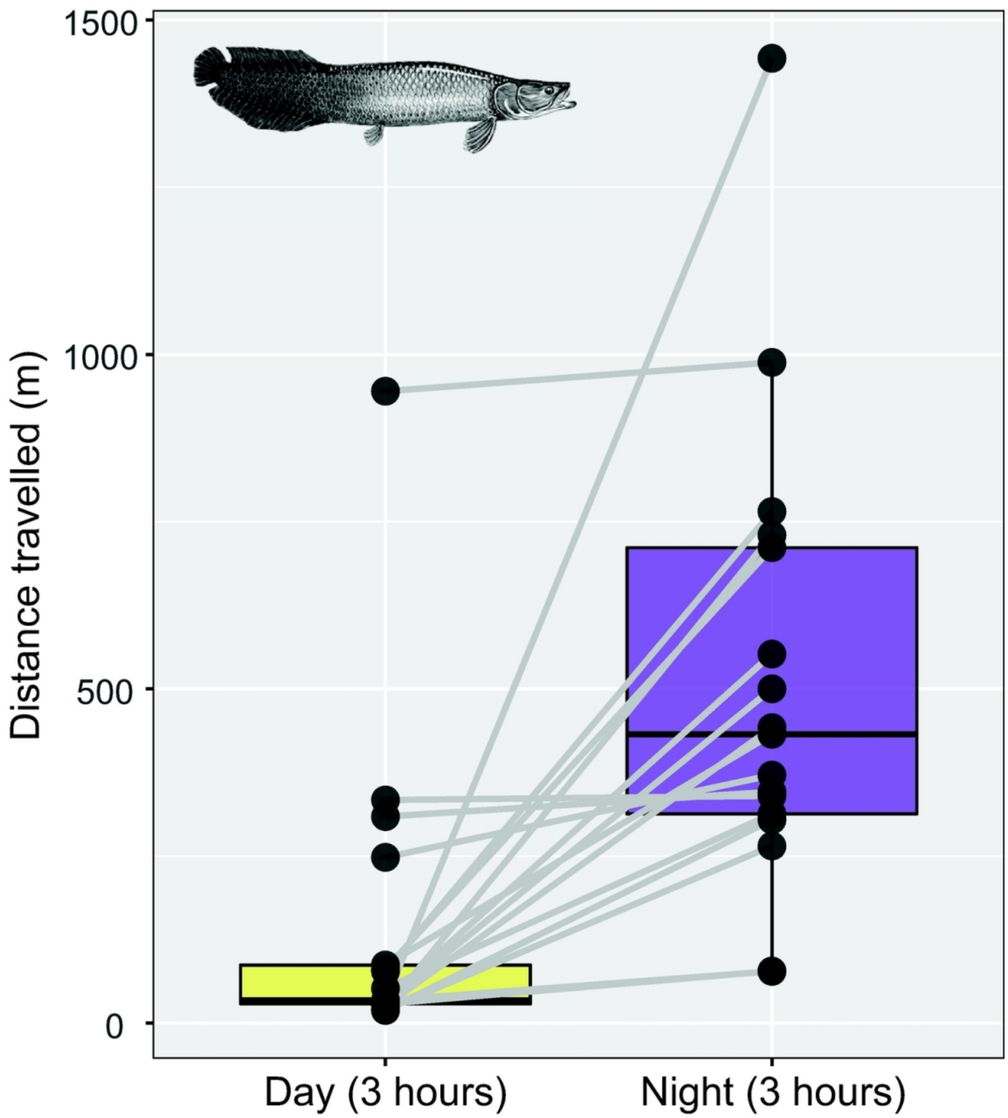

Figure 5. Effect of the diurnal cycle on pirarucu behavior in terms of total distance travelled (m) by individual pirarucu (N=13) during a three-hour observation session; boxplots and connected points show the paired design, comparing day (yellow) and night (purple) activity samples from the same individuals.

122x136mm (300 x 300 DPI)

Supporting Information

Population recovery, seasonal site fidelity and daily activity of pirarucu (*Arapaima* spp.) in an Amazonian floodplain mosaic

João Vitor Campos-Silva, Joseph E. Hawes and Carlos A. Peres

Table 1. Population census and recovery estimates for pirarucu (*Arapaima* spp.) in 29 protected lakes along the Juruá River, Amazonas, Brazil. Protected Area (PA) status gives the location of each lake inside or outside a formal PA (RDS Uacari/RESEX Médio Juruá); Current population size is from the last census in 2016, including adults and juveniles; Population in Year 1 represents the first population census in each lake; Density was calculated for both 2016 and Year 1 by dividing the respective population size by lake area; Years of protection gives the number of years of protection prior to 2016; Population increase (fold) was calculated by dividing the population in 2016 by the population in Year 1; Total (G_N) and Annual population growth rates (Ann. G_N) were calculated following the equations provided in the Methods.

Lake name	PA status	Lake area (ha)	Pirarucu population in 2016	Density in 2016	Pirarucu population in Year 1	Density in Year 1	Years of protection	Population increase (fold)	Total population growth rate (G_N)	Annual population growth rate (Ann. G_N)
Anaxiqui	PA	173	624	3.61	198	1.14	7	3.15	2.15	0.18
Aruanã	PA	16	135	8.44	70	4.38	3	1.93	0.93	0.24
Bom Fim	PA	220	436	1.98	310	1.41	7	1.41	0.41	0.05
Boto	PA	92	346	3.76	146	1.59	6	2.37	1.37	0.15
Braga	Outside	25	359	14.36	176	7.04	4	2.04	1.04	0.20
Branco I	PA	15	148	9.87	30	2.00	7	4.93	3.93	0.26
Branco II	Outside	255	142	0.56	77	0.30	4	1.84	0.84	0.17
Camponesa	PA	13	111	8.54	35	2.69	5	3.17	2.17	0.26
Cumprido	Outside	12	146	12.17	64	5.33	4	2.28	1.28	0.23
Dona Maria	PA	101	50	0.50	62	0.61	5	0.81	-0.19	-0.04

Grande I	Outside	88	1354	15.39	473	5.38	4	2.86	1.86	0.30
Grande II	Outside	294	289	0.98	84	0.29	4	3.44	2.44	0.36
Jaraqui	Outside	38.2	205	5.37	10	0.26	4	20.50	19.50	1.13
Macaco	PA	53	427	8.06	86	1.62	7	4.97	3.97	0.26
Manariã	PA	293	2878	9.82	234	0.80	1	12.30	11.30	11.30
Mandioca	PA	200	414	2.07	197	0.99	7	2.10	1.10	0.11
Marari Grande	PA	269	1376	5.12	777	2.89	7	1.77	0.77	0.09
Mutum	Outside	22	272	12.36	85	3.86	4	3.20	2.20	0.34
Onças	PA	11	114	10.36	17	1.55	4	6.71	5.71	0.61
Pirapitinga	Outside	6	342	57.00	94	15.67	4	3.64	2.64	0.38
Preto	PA	54	285	5.28	92	1.70	9	3.10	2.10	0.13
Rato	PA	335	516	1.54	250	0.75	7	2.06	1.06	0.11
Recreio	PA	86	236	2.74	32	0.37	4	7.38	6.38	0.65
Sacado do Jaburi	PA	412	1026	2.49	34	0.08	7	30.18	29.18	0.63
Sacado do Mari-mari	PA	282	230	0.82	42	0.15	5	5.48	4.48	0.41
Samauma	PA	105	586	5.58	49	0.47	7	11.96	10.96	0.43
Torcate	PA	108	116	1.07	100	0.93	7	1.16	0.16	0.02
Tracajá	PA	14	53	3.79	53	3.79	5	1.00	0.00	0.00
Veado	PA	183	496	2.71	208	1.14	4	2.38	1.38	0.24