Use of space as an indicator of social behavior and breeding systems in the gymnotiform electric fish *Brachyhypopomus pinnicaudatus*

Manuela Miranda · Ana C. Silva · Philip K. Stoddard

Abstract Extreme sexual dimorphism suggests that the South American electric fish, *Brachyhypopomus pinnicaudatus* Hopkins (Copeia 1991:151–161, 1991) is polygynous. No field studies have been conducted on the social behavior of this common gymnotiform species, in part because their nocturnal habits and densely vegetated habitat precludes direct observation in the field. We conducted mark–recapture studies on *B. pinnicaudatus* in Uruguay to gather indirect evidence of their breeding system. Sex ratios of adults were highly skewed toward females 2–3 weeks into the breeding season. Females moved twice as far as males on average ($p=0.016$) and movement tracks of individual females overlapped one another but those of males did not. These data support the hypothesis that *B. pinnicaudatus* is polygynous or polygynandrous, and suggest that they use space in a manner consistent with exploded lek polygyny or iteroparous nest site polygynandry models. Fish detected within 2 m of each other were more aggregated than chance, both day and night, suggesting they maintain social groupings or alerting networks.

Keywords Social system · Breeding system · Behavior · Sexual selection · Mark–recapture · Field study

M. Miranda · P. K. Stoddard (✉)
Department of Biological Science,
Florida International University,
11200 SW 8th St,
Miami, FL 33199, USA
e-mail: stoddard@fiu.edu

A. C. Silva
Facultad de Ciencias,
Instituto de Investigaciones Biológicas Clemente Estable,
Montevideo, Uruguay

Introduction

Gymnotiform electric fish are used as model organisms for understanding the integration of behavior and physiology. These nocturnal fish produce an electric organ discharge (EOD) that allows them to sense objects by active electrolocation (Lissmann 1958; Lissmann and Machin 1958) and to communicate among conspecifics (Black-Cleworth 1970; Hopkins 1974a, b). The New World order Gymnotiformes includes five families: Gymnotidae, Hypopomidae, Rhamphichthyidae, Eigenmanniidae, and Apteronotidae (Mago-Leccia 1994; Albert 2001). Gymnotiforms range geographically from the Chiapas province of Mexico to the Rio de la Plata system of South America (Lozano-Vilano and Contreras-Balderas 1987; Silva et al. 2003).

At the southern border of its geodistribution in South America (30–33°S), *Brachyhypopomus pinnicaudatus* breeds during the Austral summer, November–January (Silva et al. 2003). *B. pinnicaudatus* (Hopkins 1991) emits a biphasic EOD and exhibits morphological and electrophysiological sexual dimorphism during the breeding season (Hopkins et al. 1990; Caputi et al.

1998; Silva et al. 1999). Males are larger than females and emit longer lasting EODs (Hopkins et al. 1990; Hopkins 1991). The extreme sexual dimorphisms of *B. pinnicaudatus* led Hopkins and colleagues (1990) to propose that these sex differences have been shaped by sexual selection. Several studies support this proposition. For instance, gravid females move towards large males with larger EODs over small males (Curtis and Stoddard 2003). Under breeding conditions, circadian rhythms in EOD parameters are larger in males than in females (Silva et al. 2007; Stoddard et al. 2007), and plasticity of these rhythms is strongly influenced by social factors (Franchina et al. 2001; Silva et al. 2007).

A rich literature has emerged on the physiology, neuroendocrinology, sensory-motor control, and other internal processes in *B. pinnicaudatus*, over 30 publications to date. However, few published data exist on the ecology of this species or on its behavior in the field, and not one study has explored the social system directly. Therefore, our goal was to understand the nature of the social organization and breeding system of *B. pinnicaudatus*.

Friedman and Hopkins (1996) commented on the difficulty of tracking individual electric fish in the wild. *B. pinnicaudatus* is strictly nocturnal, inhabiting shallow bodies of muddy water densely covered with aquatic plants. Three field methods are useful to obtain data that can be used to infer behavioral patterns: electric probe census, capture census, and mark recapture studies. Electric probe census can provide data on dispersion and space use, location of fish relative to the nesting and foraging habitat, and fish density, though sex cannot be readily determined from acoustic transformations of the EOD (Hopkins and Heiligenberg 1978; Crampton 1996; Friedman and Hopkins 1996; Crampton 1998). Capture census can provide data on sex ratio, dispersion of the sexes, sizes of individuals, and sex differences in physical injuries such as incidence of tail damage (Hopkins et al. 1990). A capture study may be biased by differential ease of capture across age or sex classes. A mark–recapture study can provide additional information such as movement patterns and distances of the sexes, and location of the sexes relative to their resources, such as plant cover used for nesting or foraging. Data obtained on behavior of electric fish under typical field conditions will necessarily be circumstantial rather than a direct observation of the breeding behavior itself (e.g., Crampton and Hopkins 2005).

Breeding systems can be classified with respect to the operational sex ratio (Reynolds 1996), as well as the resources necessary for breeding such as spatial distribution of food, mates, and breeding sites (Emlen and Oring 1977; Andersson 1994; Schuster and Wade 2003). Thus, the comparison of movements between the sexes as well as the sex ratio can either support or discount possible breeding systems (Table 1). According to Emlen and Oring (1977), in scramble competition polygyny, for example, where males move around searching for dispersed females, we would expect to find that males exhibit large overlapping home ranges. In exploded leks we would expect to

Table 1 Different breeding systems are associated with different patterns of movement and use of space by the two sexes

Breeding system	Description	Expected movement patterns
Monogamy	One male mates with one female in a breeding season	Male and female stay together or return to same place.
Polygynandry	Both sexes have several partners in a breeding season	Both sexes move around seeking mates.
Mate defense polygyny	Males guard groups of females	One male stays close to stable group of females.
Resource defense polygyny	Males with defensible resources attract females	Males guard territory and females move around or settle with chosen male.
Scramble competition polygyny	Males good at finding females become polygynous	Males move extensively seeking multiple females.
Classic lek polygyny	Males display and show non aggressive behaviors	Aggregated and stationary males wait for spawning females.
Exploded lek polygyny	Males display and are aggressive and territorial	Dispersed males defend sites and wait for females.

These are provided for later comparison against movement patterns detected within our mark–recapture data. Modified from Alcock (2005) and Schuster and Wade (2003).

find essentially the opposite pattern where males overlap little but females cover the ranges of multiple males. Recognizing the inherent methodological limitations of fieldwork on electric fish, we carried out a field study to analyze the use of space and movement of *B. pinnicaudatus* in the wild and to infer details of their behavior and breeding system.

Materials and methods

Study locations

We studied *B. pinnicaudatus* in five sample plots (SPs) located in three bodies of water in the eastern and western areas of Uruguay (Fig. 1): Laguna las Lavanderas, Department of Tacuarembó (31°42′S, 55°58′W, SP1); Laguna Lavalle, Department of Tacuarembó (31°48′S, 55° 13′W, SP2, SP3, and SP4), and Laguna el Tigre, Department of Treinta y Tres, (33°18′S, 54°35′W, SP5). Following Silva et al. (2003) who identified the breeding season for this species at these latitudes from November to February, we collected field data during breeding in two field expeditions conducted with different purposes: (a) the assessment of day–night spatial aggregation in Laguna el Tigre (6–14 Dec 2004); and (b) the detection of movement patterns across the sexes in Laguna las Lavanderas and Laguna Lavalle (19–24 Nov 2006).
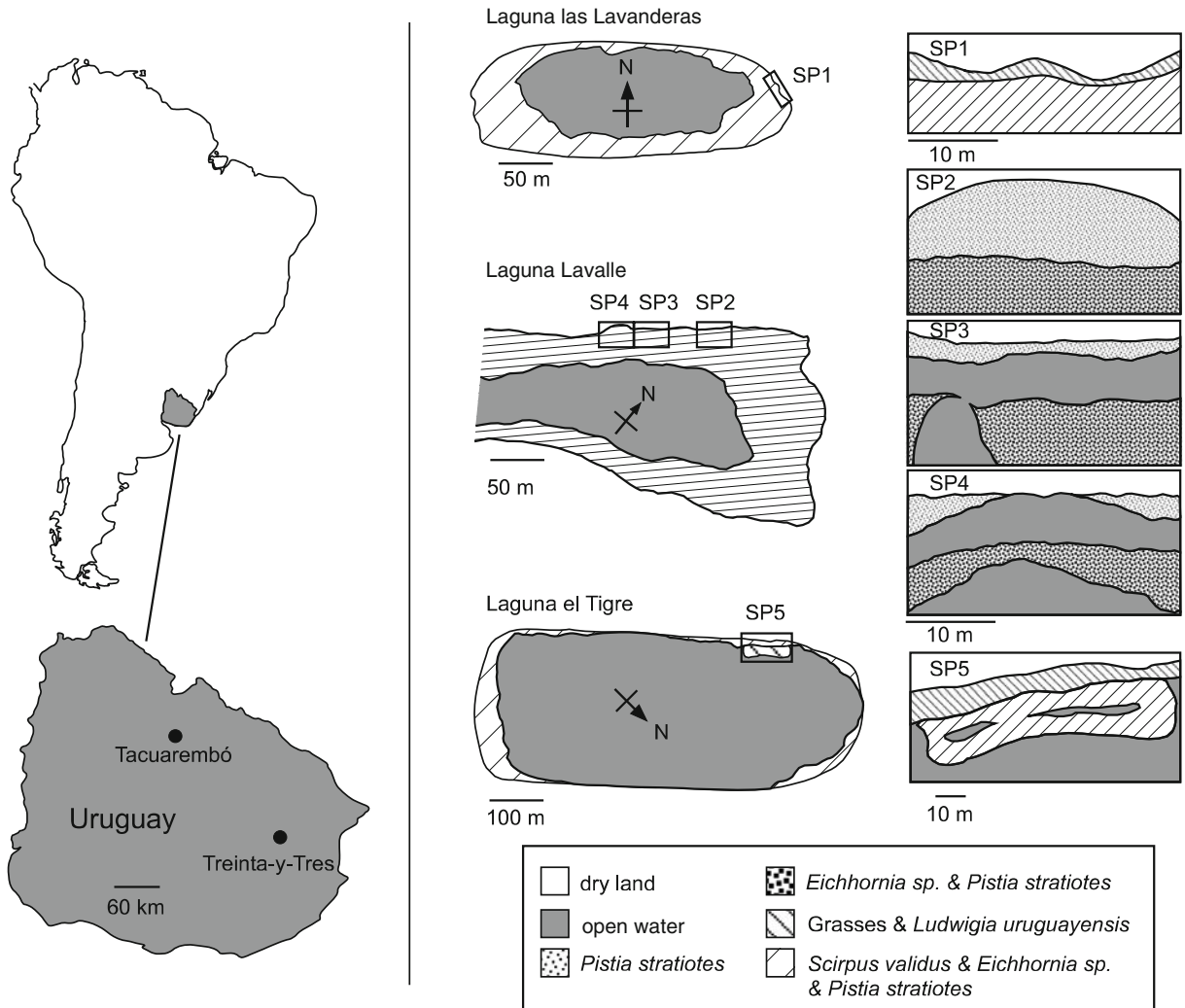

Fig. 1 Schematic representation of study areas and their respective sampling plots: Laguna las Lavanderas (SP1); Laguna Lavalle (SP2, SP3, SP4); Laguna el Tigre (SP5)

All three study areas showed similar characteristics: water depths <1 m, low water conductivities <55 µS cm^{-1}, high daytime water temperature ranging from 22.7 to 27.3°C around noon, and dense and even aquatic macrophyte cover of *Ludwigia uruguayensis*, *Pistia stratiotes*, *Scirpus validus*, *Eichhornia sp.*, and thick grass mats.

We took advantage of gymnotiform electric signals for detecting and collecting fish. Our fish detector, comprised of a portable electrode–amplifier–loud-speaker assembly, detected the signal of electric fish from a distance of up to 2 m. As the transformed signal of the fish became audible, we carefully located its hiding place and gently captured the fish with a 1 m diameter hand net. We collected fish from comparable sample plots (SP1-SP4, Fig. 1) defined by 30 m-transect lines on shore, using a total effort of 2 h per capture plot.

Electric probe census to assess spatial aggregation by day and night

We selected a naturally defined area of Laguna el Tigre, 90×24 m, (SP5, Fig. 1) covered by thick vegetation and inhabited by a dense congregation of *B. pinnicaudatus*. We waded through each sample plot in a zigzag fashion exploring the presence of electric fish with the fish detector. The pitch and timbre of the acoustic transformation of EODs through the audio speaker allowed us to identify isolated fish and dyads. When more than two fish were close together (<30 cm) we could not determine the precise number of fish by the acoustic rendition. In such cases we assigned the presence of three fish whenever we heard more than two within the range of the electric probe. We noted each fish position relative to the transect line on shore and the distance to shore. We conducted this procedure during the day (16:00–18:00 h, 10 Dec 2004) and at night (21:30–23:30 h, 12 Dec 2004).

Our subjective impression from the electric probe census was that *B. pinnicaudatus* were aggregating in groups less than a meter across. To test whether the aggregation differed from random, we calculated nearest neighbor distances for the 109 fish censused in the day and the 97 fish censused at night. From these we calculated day and night histograms of nearest neighbor distances with bins 1 m wide. We compared these against a distribution of distances obtained from a 100,000 iteration Monte Carlo simulation of nearest neighbor distances with random placement. To create the randomized spatial distributions, we randomly assigned the same number of fish to continuously distributed locations along the shoreline in the same overall density as found in the census, computing nearest neighbor distances for each randomly placed individual, and histograms as above. We conducted separate randomization tests for day and night data. We used a chi-square test to compare number of fish in the 0–1 and 1–2 m bins of the data histograms against the means of the same bins obtained from histograms of 100,000 randomly generated data sets.

Mark–recapture study for detecting movement patterns across the sexes

We carried out mark–recapture studies at two sites, Laguna las Lavanderas (SP1) and Laguna Lavalle (SP2, Fig. 1). At each site we flagged a 30 m transect line on shore to serve as X-coordinate for the plot. The Y-coordinate was distance from shore (Fig. 1), typically limited by the practical limit of depth at which we could work, ~1 m. Sample plots were open to dispersal of fish between adjacent areas of contiguous plant cover outside the plot. During the marking session, fish were detected, captured, sexed, measured, and marked at the site of capture. We determined sex by visual inspection of sexually dimorphic characters (longer, thicker tail in males, visible eggs in females). We measured the fish's total length using a digital caliper. Each fish was quickly marked by clipping a small nick in the elongated anal fin that runs the length of the body. Individual fish could be identified by a unique combination of total length and position of the fin clip on the anal fin. Prior observations of fin-clipped fish in lab aquaria showed that they swam normally and that the clips remained visible for more than 1 week. At each site where a fish had been caught we planted a flagged plastic pole marked with the fish's ID number and measured the distance to shore to serve as the Y-coordinate. When all fish were marked we released them at their sites of capture. We took 3 h to capture, fin clip, and measure a total of 20 fish in a marking session.

After the initial capture and marking session, we conducted four recapture sessions at each site, two in

the day and two at night. To minimize fish disturbance, we never conducted day and night recapture sessions in the same plot on the same date. At SP1 we carried out day sessions at 10:30–14:00 on 20, 21, 24 Nov 2006 and night sessions at 21:00–23:00 on 22 and 23 Nov 2006. At SP2 we carried out day sessions at 10:00–18:00 on 19, 22, 23 Nov 2006, and night sessions at 21:00–23:00 on 20 and 21 Nov 2006. We waded systematically through the sample plot listening for every electric fish with the electric fish detector. We attempted to capture each fish detected. We measured marked fish (total length and nick position) and their respective ID and recorded their locations. We retained all fish captured at the site of capture (no more than 30 min) while we rechecked the entire plot twice to capture any stragglers. On completion we returned the fish to their sites of recent capture.

We compared movement patterns and distances of male and female *B. pinnicaudatus* using mark–recapture data from SP1 and SP2. Some fish were captured twice or more. To obtain the representative movement distance of fish that were recaptured more than once we took the greatest distance between the multiple capture points. Movement distances were log & square root transformed to normality prior to parametric statistical tests. To compare means for males and females, we bootstrapped a 50,000 iteration two-sample *T*-score distribution assuming unequal variance using MATLAB V. 7.4, Statistics Toolbox V. 6.0 (Mathworks, Natick, MA). We pooled distances across the sexes and, in each iteration, selected random samples to represent the two sexes, and then calculated a *T*-score for the difference between means. The subsequent *T*-test of obtained data was compared against the two-tailed distribution of *T*-scores from randomized data.

Sympatric species control for effects of disturbance

We sought to differentiate whether the movements of marked individuals were the result of natural dispersion behavior or were caused by our own disturbance of the vegetation. In Laguna Lavalle census work for a different study of population density revealed three different gymnotiform species within two of the three study plots we used: *B. pinnicaudatus*, *Brachyhypopomus bombilla* (Loureiro and Silva 2006), and *Gymnotus* n. sp. *'omari'* (Richer-de-Forges, personal communication). The presence of these species provided the possibility of a control for investigator disturbance to the habitat. If *Gymnotus* were to abandon their capture sites (Black-Cleworth 1970) that would indicate our disturbance had made the capture site unsuitable or insecure for habitation, forcing the fish to move around. *Gymnotus* was repeatedly found and easily captured in the same marked spots, never in uninhabited intermediate locations with similar vegetation. These fish were not marked, but whether they were the same individuals or not, clearly the disturbance from passage of human feet during the electric probe census did not make the spots unsuitable for habitation. Continuous mats of the floating macrophyte *Pistia stratiotes* repaired themselves after our disturbance, in contrast to the rooted vegetation in which *Gymnotus* resided. For these reasons, we believe movements of *B. pinnicaudatus* between successive mark–recapture trials were not unduly influenced by our activities and thus we conclude that the movements we saw resulted from their normal use of the habitat.

Results

Habitat use

B. pinnicaudatus were only found in areas of dense aquatic plant cover (*Ludwigia uruguayensis*, *Pluchea sagittales*, *Scirpus validus*, *Eichhornia sp.*, and *Pistia stratiotes*; see Fig. 1). We detected no fish in an area dominated by *Scirpus validus*, a plant that provides no hiding places for fish. Likewise we detected no fish in open water absent of vegetation.

Dispersion vs. clumped spatial distributions

B. pinnicaudatus were aggregated during the day and night. In Laguna el Tigre SP5, the numbers of individuals closer together than 1 m was higher than predicted by randomization models, and the numbers 1–2 m apart were depressed below the values predicted by random models (Fig. 2, day: chi-square=31.58, $p=1.9\mathrm{e}{-}08$; night: chi-square=25.81, $p=3.8\mathrm{e}{-}07$). Greater nearest-neighbor distances conformed to the random models. These findings suggest that fish prefer to aggregate at distances below 1 m.
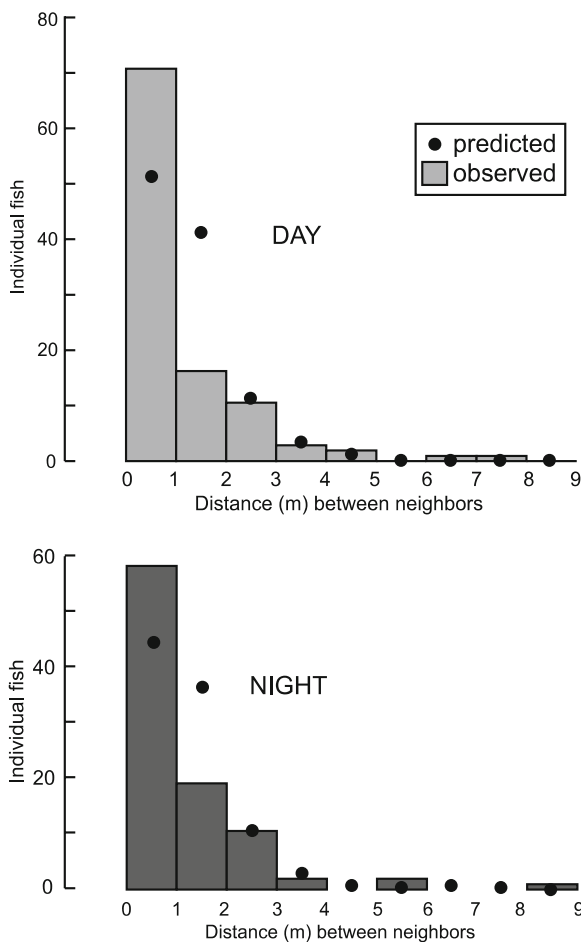
Fig. 2 Nearest neighbor distances between *Brachyhypopomus pinnicaudatus* determined by electric probe census during day and night two-hour surveys. Fish were more commonly found within 1 m of one another than expected by chance, and less frequently found 1–2 m apart than predicted by chance. This pattern suggests aggregation of individuals within 2 m of one another. Curiously, aggregation was more extreme by day when the fish were sedentary than at night when they were active

Sex ratios

Across our sample, females outnumbered males by about 3-to-1 (43 females: 16 males, though ratios at individual plots varied from 1.75:1 to 5:1; Fig. 3). Juveniles were found only in SP1 (Laguna las Lavanderas) and SP2 (Laguna Lavalle). Both males and females were caught in almost all day and night trials. Of the 40 fish marked (eight males, 32 females), we recaptured 24 at least once (four males, and 20 females). No significant or even suggestive sex bias is apparent in these recapture data (Table 2), indicating that the observed skew in sex ratio was not due to sex differences in ease of capture.

Movement patterns and distances of male and female *B. pinnicaudatus*

Mark recapture data revealed that males *B. pinnicaudatus* move shorter distances than females (Figs. 4 and 5, Table 2). Marked fish were always recaptured less than 20 m from previous capture sites and we never recaptured marked fish that had crossed between the plots (two plots were adjacent, the third was separated by 30 m). Movement lines of individual females crisscrossed the area and the movement lines of other females (Fig. 4), a pattern consistent with their use of wide and undefended home ranges. With a single exception, movement lines of males did not cross those of other males. This pattern of limited overlap is more consistent with territorial defense by males.
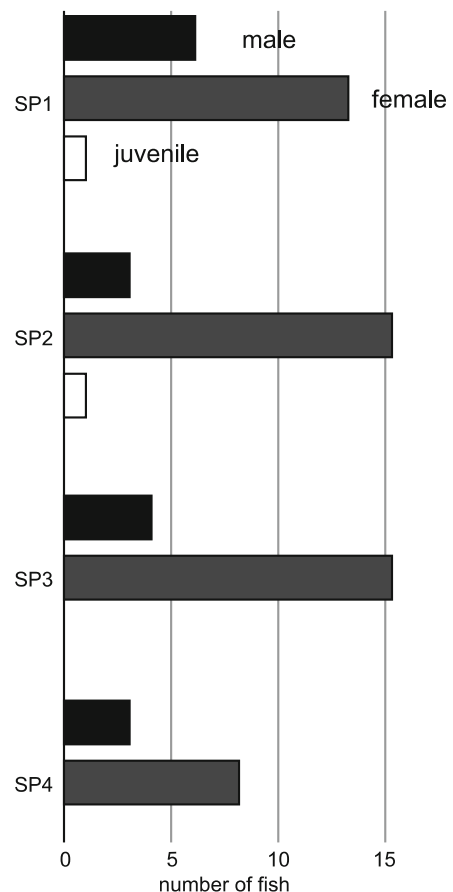

Fig. 3 *Brachyhypopomus pinnicaudatus* captured in different SPs of Laguna las Lavanderas and Laguna Lavalle. More females than males were captured in all four study plots. Juveniles were only found on SP1 and SP2

Table 2 Data summarized from mark–recapture experiments in SP1 and SP2 reveal a strong female bias in the sex ratio, but no sex bias in recapture rates

	Males	Females	Sex ratio
Total marked	8	32	1:4
Total recaptured	4	20	1:5
Fraction recaptured	0.500	0.625	1:1.25
Mean distance moved (m)	3.86	8.39	
SD distance moved (m)	2.28	5.63	

Had a single additional male been recaptured, the fractions recaptured would have been identical across the sexes. In no case is the sex bias in recapture data of sufficient size to account for the highly skewed sex ratios found at these sites. On average, females moved more than twice as far as males between recaptures.

Discussion

This study expands our prior knowledge of the natural history of a poorly understood group of fish. Although our data are limited, we believe they are sufficiently important and useful to create novel hypotheses and encourage starting points for future studies and further investigations.

Skewed sex ratio of *B. pinnicaudatus*

Two to three weeks into the breeding season, which lasts about 3 months (Silva et al. 2003); we discovered an unexpected female-biased sex ratio (Fig. 3). We consider six alternate explanations for a sex bias in capture ratios. (a) It is possible that males are harder to catch than females resulting in sex-biased capture data. However, we looked for sex biases in recapture of marked individuals and found none: males and females were recaptured with similar frequency (Table 2). (b) Males in the field might not have sexually differentiated, and thus were classified as juveniles or misclassified as females. However, of 40 fish marked, only two were juveniles. The rest were either gravid females or fully differentiated males. Further, we captured mature male and female *B. pinnicaudatus* of different sizes in both Laguna Lavalle and Laguna las Lavanderas. Thus we discount delayed maturation as a possibility. (c) Males may have been residing somewhere we could not detect or capture them. We found that males were spread out with no apparent segregation by size; e.g., three males ranging from 11 to 20 cm in total length were caught almost equidistant from each other in SP1 (around 2 m, Fig. 4). Moreover, sizeable areas existed with females but no males (Fig. 4). Thus it seems unlikely that smaller males were residing in marginal areas where they were neither detected nor caught. (d) Because the study plots were contiguous with other areas, males might have emigrated from our study plots into newly flooded areas. However, we saw the same scarcity of males in closed systems, such as a small marsh adjacent to Laguna el Tigre, which discounts emigration as a likely explanation. (e) A skewed primary sex ratio could have resulted in the female biased sex ratio found in our study plots. No field data exist on the sex ratio of *B. pinnicaudatus* outside the breeding season when they lack externally visible sexual dimorphism. However, the sex ratio in lab-reared populations is close to unity (Stoddard lab, 15 years of unpublished breeding data), so the depressed number of males in the field is not likely caused by a skewed primary sex ratio. (f) Males might have died earlier in the breeding season than females, possibly from differential predation, or effects of energetic expense or immunosuppression. Males could expend substantial energy in mating while feeding less, or they could be fighting intensely at the onset of the breeding season. Males are also thought to be more prone to predation because of their highly conspicuous electric signals (Stoddard 1999, 2002). Males are more prone to stress-related mortality in captive breeding and maintenance pools than either females or juveniles (Stoddard unpublished data). Fighting, indirect effects of competition, or predation could increase male mortality earlier in the breeding season. We did not find males with the tail injuries described by Hopkins et al. (1990), though we did find females with injured anal fins.

Because we cannot account for the missing males, we suspect males show a high level of mortality very early in the breeding season, perhaps as an indirect

Fig. 4 Mark–recapture data indicate positions and movements of individual fish. *Lines* between points represent successive captures of individuals. Females can be seen to move considerable distances and to cross one another frequently. Males tend not to overlap, and their distances moved are shorter
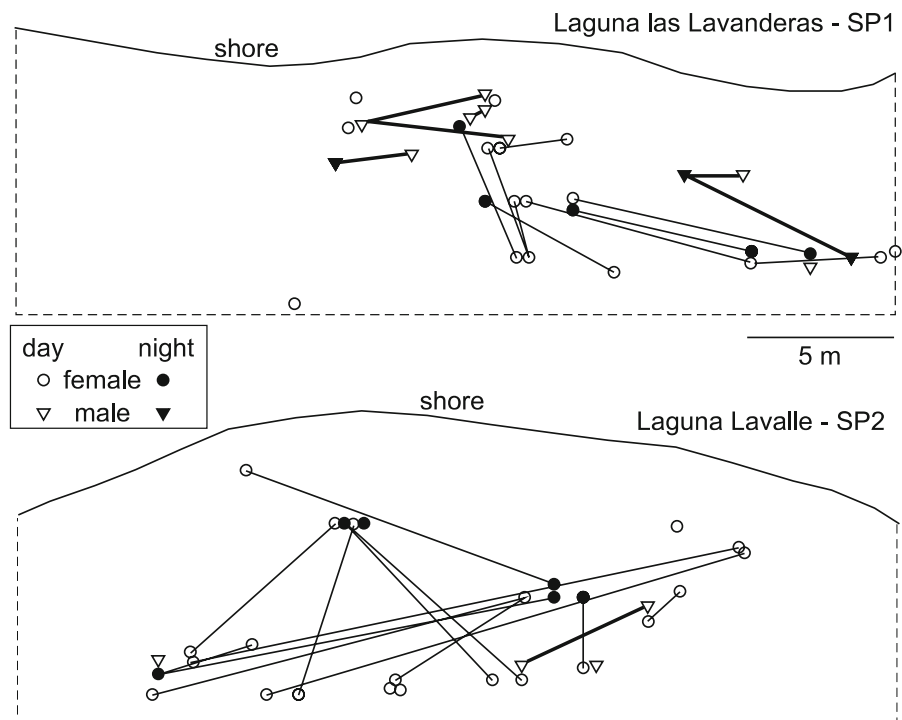
consequence of the stress of competition. If male mortality is the cause of the skewed sex ratio we observed, it would suggest that competition among males is intense at the onset of breeding, then relaxes among the few surviving males for the remainder of the season. A mark–recapture study initiated before the onset of the breeding season might provide a clearer picture of this phenomenon. Though the cause of male disappearance remains unknown at this time, any explanations would be consistent with the high degree of sexual selection typical of some sort of polygynous breeding system.

Discrimination between possible breeding systems

The movement data collected in the mark–recapture study allow us to compare sex differences in spatial use by *B. pinnicaudatus* against the patterns typical of different breeding systems (Table 1). Importantly, females moved significantly greater distances than males and movements of females overlapped each other considerably whereas movements of males did not (Figs. 4 and 5).

Sex differences in these directions are inconsistent with scramble competition polygyny, female defense polygyny, or monogamy. The wide distribution of

similar plants suitable for ovoposition is not consistent with resource defense polygyny in which males defend limited ovoposition sites. Neither the wide roaming of females nor the wide distribution of plants where invertebrate food might be found is consistent with resource defense polygyny in which males defend limited foraging sites. The wide spatial distribution of males across the marshes (Fig. 4) is not consistent with classic lek polygyny, for which we would expect to see a tight cluster of males occupying a small section of each marsh. In exploded leks, males display and defend territories at particular sites where they may attract or encounter receptive females (Schuster and Wade 2003). Iteroparous exploded lek polygyny is consistent with the observed movement patterns across the sexes of *B. pinnicaudatus* in Uruguay.

In the lab, a well-fed female will spawn once a week (Stoddard lab, unpublished data), and in the field, females appeared gravid throughout our field study, consistent with lab observations of fractional spawning. Thus a female has the opportunity to mate serially with multiple males across the breeding season. Mature males in the lab are willing to spawn every night, though in the field, most males had apparently disappeared earlier in the breeding season.
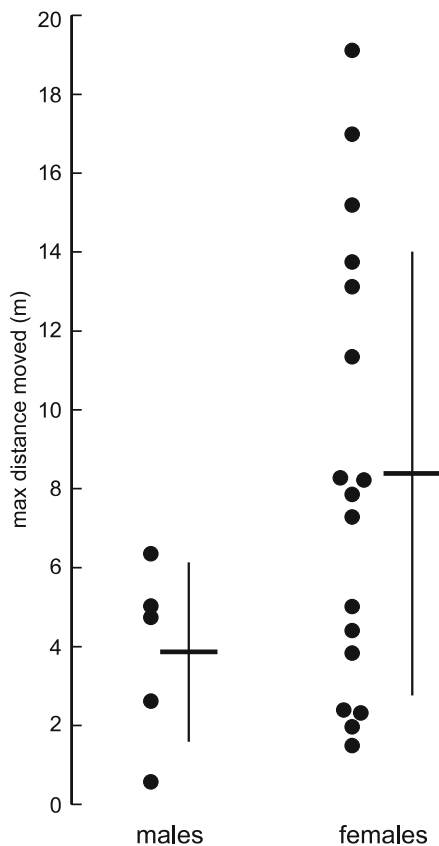
Fig. 5 Maximum distances moved by both male and female *Brachyhypopomus pinnicaudatus*. This graph shows maximum distances moved by recaptured individuals in SP1 and SP2 during day and nighttime captures (*dots*) along with means and standard deviations (*lines*). Females move significantly greater distances than males (males: 3.86 m±sd 2.27, females: 8.38 m ±sd 5.62, *p*=0.016, 2-tailed)

A change in demographics like this must have a significant effect on female behavior. If the sex ratio is unity at the start of the season, as lab rearing suggests, the operational sex ratio would be male biased, a classic predictor of polygyny. With the sharply female biased sex ratio that we observed a few weeks into the breeding season, the operational sex ratio would have reversed, perhaps causing females to compete for male attention, since spawning can take up to 2 h. While a fractional spawning female would have the opportunity to mate with multiple males across the breeding season, she would have little choice but to do so if a preferred male disappeared early on. Thus, some form of polygynandry might result as the ultimate breeding system for this species.

The exploded lek system is typically described for animals with parental care, where the female mates with the male and departs to raise her young elsewhere (Schuster and Wade 2003). This aspect does not readily fit any animal with external fertilization. No parental care has been noted for *B. pinnicaudatus* in dozens of breeding episodes observed in the lab (Kirschbaum and Schugardt 2002; Stoddard unpublished data). Rather, female *B. pinnicaudatus* conceal their eggs at a site of the male's choosing by ovipositing in cavities and behind submerged leaf bracts. It is possible, but unlikely that males directly protect these cryptic ovoposition sites from nest predators, though they may do so indirectly through territorial defense. Any nest defense, direct or indirect, might make iteroparous nest site polygynandry a better fit for this species (Schuster and Wade 2003).

A mark–recapture study of the congener *Brachyhypopomus occidentalis* in small streams in Panama found that females showed site fidelity while males moved around the stream, as far as 130 m downstream from the original capture site (Hagedorn 1988). Sex differences in movement patterns of *Brachyhypopomus occidentalis* suggest scramble competition polygyny in which females are stationary and males move among multiple females. This is precisely opposite the pattern we found in its congener *B. pinnicaudatus*. Taxonomic differences of this sort are to be expected, but given the extremely wide latitudinal distribution of *B. pinnicaudatus*, from Guyana to Uruguay, we would not be surprised to find similar differences exist within the species (or what is currently considered to be the species).

Spatial aggregation of *B. pinnicaudatus* as a possible daytime anti-predator network

Distributions of *B. pinnicaudatus* in Laguna el Tigre (SP5) during the day and night showed significantly more clumping than predicted by randomization models. This clumping can be seen as more fish in the 0–1 m range and fewer in the 1–2 m range than predicted (Fig. 5). The uniformity of the vegetation in which they were found does not support the idea that they clumped because of habitat structure. The logical alternative is that these fish clumped by deliberate choice of proximity to neighboring individuals. Most gymnotiforms with pulse-type discharge patterns, including *B. pinnicaudatus*, increase their discharge rates when disturbed, which allows them to image

their world more accurately through active electro-location (Caputi et al. 2003). Such a "novelty response" as it is called, may indirectly alert nearby individuals to possible danger. A fish thus alerted, could unwittingly alert neighbors within range to detect its EOD. A similar social network is used by breeding assemblages of red-winged blackbirds in which males change their ongoing train of calls when they sense a disturbance, thereby alerting their mates and neighboring males, who pass on the message in a wave of changes across the marsh (Beletsky et al. 1986). To enjoy the benefits of an alerting network, electric fish would need optimal spacing. If they are too close (e.g., within a body length), they interfere with each other's electrosensory systems. If they are too far (e.g., beyond half a meter) they become electrically isolated from neighbors. The frequently observed spacing within 30 cm may be optimal for operation of an alerting network.

Summary/Conclusions

This study has shown the feasibility of studying social behavior of a nocturnal gymnotiform electric fish, *B. pinnicaudatus*, in its virtually opaque natural habitat. Where the aquatic vegetation was robust to distur-bance, we were able to track the movements of individuals through repeated electric census and mark–recapture trials without destroying the habitat and displacing the animals. Electric census in Uru-guay showed that, during the Austral breeding season, individual *B. pinnicaudatus* were more spatially clumped than expected by chance, both during the day and night. The most common distance between individuals was less than 1 m, and was estimated to be about 1/3 m. This spatial aggregation occurred at a scale finer than could be accounted for by the apparent scale of vegetation patchiness, and thus indicates *B. pinnicaudatus* engages in some sort of social aggregation, both by day when it rests and by night when it is active. Mark–recapture showed that males moved up to 6 m (mean 3.9 m), whereas females moved significantly greater distances, up to 19 m (mean 8.4). Lack of movement between adjacent census plots indicated fish were not moving greater distances. Movements of individual males did not overlap, thus suggest exclusive home ranges or perhaps defended territories. Movements of females overlapped each other and the ranges of multiple males, suggesting nonexclusive home ranges and the likelihood of social interaction with multiple males. When this study was initiated, three weeks into the breeding season, the sex ratio was highly biased toward females. The same pattern was seen in multiple sites including those with no possibility of emigration. The missing males were presumed dead, perhaps a casualty of intense intrasexual competition in the first weeks of the breeding season. The overall pattern suggests *B. pinnicaudatus* in Uruguay has a polygynous or polygynandrous mating system per-haps resembling the exploded lek or iteroparous nest site polygynandry models. While this study cannot be considered comprehensive, it provides our first insights into the natural social behavior of this widely distributed gymnotiform electric fish, and shows what is possible to study under natural conditions.

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