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Acknowledgements Discussions with C. Wunsch, J. Marshall, M. Follows, E. Boyle and P. Parekh contributed to this manuscript. Samples from core MD97-2120 were provided by K. Pahnke and R. Zahn. The Lamont-Doherty Earth Observatory core repository provided samples from core TN057-21-PC2. D. Dryer, M. Fleisher, Y. Chang and M. Bryan assisted with laboratory analyses. Funding for J.P.S. was from the Gary Comer Foundation, the Jeptha H. and Emily V. Wade Award for Research, and a Henry L. and Grace Doherty Professorship. Funding for R.F.A. was from a grants/cooperative agreement from the National Oceanic and Atmospheric Administration.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to J.P.S. (jsachs@mit.edu).

Electronic tagging and population structure of Atlantic bluefin tuna

Barbara A. Block[1], Steven L. H. Teo[1]*, Andreas Walli[1]*, Andre Boustany[1]*, Michael J. W. Stokesbury[1,3], Charles J. Farwell[2], Kevin C. Weng[1], Heidi Dewar[1] & Thomas D. Williams[2]

[1]*Tuna Research and Conservation Center, Stanford University, Hopkins Marine Station, Pacific Grove, California 93950, USA*
[2]*Monterey Bay Aquarium, 886 Cannery Row, Monterey, California 93940, USA*
[3]*Dalhousie University, Biology Department, Halifax, Nova Scotia, B3H 4J1 Canada*

* These authors contributed equally to this work

Electronic tags that archive or transmit stored data to satellites have advanced the mapping of habitats used by highly migratory fish in pelagic ecosystems[1–6]. Here we report on the electronic tagging of 772 Atlantic bluefin tuna in the western Atlantic Ocean in an effort to identify population structure. Reporting electronic tags provided accurate location data[7–9] that show the extensive migrations of individual fish ($n = 330$). Geoposition data delineate two populations, one using spawning grounds in the Gulf of Mexico and another from the Mediterranean Sea. Transatlantic movements of western-tagged bluefin tuna reveal site fidelity to known spawning areas in the Mediterranean Sea. Bluefin tuna that occupy western spawning grounds move to central and eastern Atlantic foraging grounds. Our results are consistent with two populations of bluefin tuna with distinct spawning areas that overlap on North Atlantic foraging grounds. Electronic tagging locations, when combined with US pelagic longline observer and logbook catch data, identify hot spots for spawning bluefin tuna in the northern slope waters of the Gulf of Mexico. Restrictions on the time and area where longlining occurs would reduce incidental catch mortalities on western spawning grounds.

Giant bluefin tuna are the largest members of the family Scombridae, attaining body sizes of more than 650 kg (refs 10, 11). They are unique among teleosts for their endothermic capacity and cardiovascular physiology[12,13]. These traits underlie their capacity to exploit environments ranging from subarctic feeding grounds to subtropical spawning areas. Top pelagic predators such as bluefin tuna are in precipitous decline globally because of overexploitation[14]. The International Commission for the Conservation of Atlantic Tunas (ICCAT) manages Atlantic bluefin tuna as distinct western and eastern stocks separated by a management boundary at the 45° W meridian[10,11]. The spawning stock biomass of western Atlantic bluefin tuna has decreased by 80% or more since 1970 (refs 10, 11). A 20-year rebuilding plan was enacted in the early 1980s in the western Atlantic[10]. The most recent assessment indicates that the western stock continues to decline[11], yet mortality throughout the North Atlantic remains high. Key questions remain on the biology of this species. Establishing the location and timing of reproduction, the mean age of maturity, spawning site fidelity, the ontogeny of movement patterns and the influence of climate variability on movements will improve stock assessments and subsequent management[15]. Here we report the spatio-temporal distributions of Atlantic bluefin tuna determined with electronic tags, discriminate two potential spawning populations, and record spawning site fidelity to the Mediterranean Sea.

We deployed 499 implantable archival tags and 273 pop-up satellite (PAT) tags on bluefin tuna in the western Atlantic (Supplementary Information)[2,3,6]. To date, 86 archival-tagged bluefin tuna have been recaptured; 54 in the west Atlantic, 9 in the east Atlantic and 23 in the Mediterranean Sea. Twelve PAT-tagged fish were recaptured and 237 PAT tags transmitted data to Argos satellites after 2 to 251 days after tagging (Table 1). Individual tracks of 2 to 1,623 days have been obtained.

Our database comprises 13,372 positions obtained from 330 bluefin tuna that carried electronic tags from 1996 to 2004 (Fig. 1, Table 1). Geoposition data include the following: Doppler-based Argos endpoint positions calculated for PAT tags ($n = 237$)[9]; geolocation estimates for archival ($n = 5{,}171$) and PAT tags ($n = 7{,}536$), using light level and sea surface temperature (SST) to estimate longitude and latitude, respectively[9]; Global Positioning System deployment locations for recovered archival and reporting PAT tags ($n = 330$); and recapture locations from recovered archival and PAT tags ($n = 98$). The distribution of these positions across the North Atlantic Ocean indicates that the western and eastern management units are strongly linked with overlapping ranges.

The electronic tagging data reveal two populations of Atlantic bluefin tuna that overlap on North Atlantic Ocean foraging grounds and sort to independent spawning areas located primarily in the Gulf of Mexico (GOM) and Mediterranean Sea (Fig. 1). A bluefin tuna was assigned to the western Atlantic spawning unit if it visited a known western Atlantic ICCAT spawning area (GOM, Bahamas or Florida Straits) for more than 7 days in winter or spring[10,11,16–18] and

Table 1 **Electronic tags deployed in the western North Atlantic, 1996–2004**

Tag type (year)	Releases	Tagged fish recaptures	Successful pop-ups	Recovery or reporting (%)	Mean length at tagging (cm CFL)
Archival* (1996–1999)	280	77	n.a.	28	199 ± 16
Archival† (2002–2004)	219	9	n.a.	4.1	199 ± 19
PAT (1997–2004)	273	12‡	237	89	211 ± 20

n.a., not applicable.
*Archival tag models: NMT V1.1, V1.2 and WC Mk7.
†Archival tag model: Lotek LTD2310.
‡Six recaptures of PAT-tagged fish occurred after the PAT tag had been released and are also recorded as successful pop-up reporting events. Six bluefin tuna recaptures before PAT tag release are not listed in successful pop-up events. One tag did not transmit and the PAT tag was recovered on a beach.

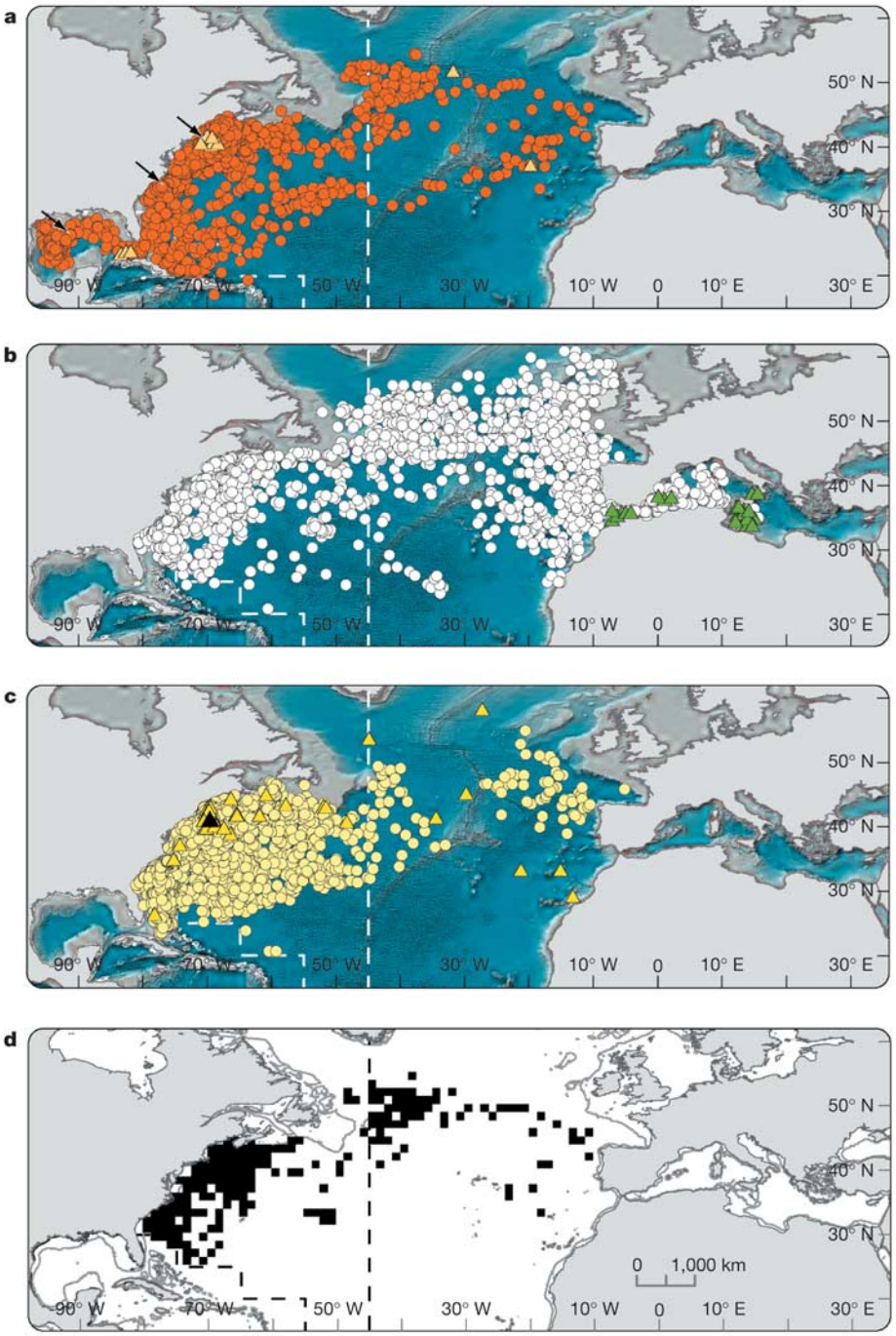

Figure 1 Positions of Atlantic bluefin tuna electronically tagged at three western Atlantic locations (arrows) during 1996–2004. Circles represent locations based on deployment positions, light-based and SST-based geolocation estimates[7–9], and PAT tag satellite endpoint positions. **a**, Fish classified as western breeders (10 archival tags, 26 PAT tags, 219 ± 27 cm CFL at release, median time at large 579 days). **b**, Fish classified as potential eastern breeders (23 archival tags, 3 PAT tags, 207 ± 17 cm CFL at release, median time at large 926 days). **c**, Fish that did not visit a known ICCAT breeding ground (53 archival tags, 215 PAT tags, 202 ± 16 cm CFL at release, median time at large 141 days). **d**, Spatial overlap of western and eastern breeders identified in **a** and **b**. The dashed line in all panels indicates the current ICCAT management boundary (45° W meridian) and western breeding zone[10,11]. Triangles represent recapture locations of electronically tagged fish; the black triangle denotes $n = 35$ recaptures.

occupied surface water temperatures of at least 24 °C, the SST reported for western spawning activity[5,18,19] ($n = 36$, Fig. 1a). Bluefin tuna that displayed transatlantic movements into the Mediterranean Sea and were recaptured in the spawning season (June to August[10], $n = 20$) or in the Straits of Gibraltar (May to August, $n = 6$) were classified as potential eastern spawners (Fig. 1b). Bluefin tuna that remained in the North Atlantic throughout the track duration without visiting the known ICCAT spawning areas were classified as neutral ($n = 268$, Fig. 1c). We compared the distributions of the 62 bluefin tuna identified as potential western or eastern spawners and calculated a spatial overlap of the positional data sets of 47% in North Atlantic waters (Fig. 1d). These mixing zones were primarily in the western and central Atlantic. Importantly, no mixing occurred in the GOM and Mediterranean spawning areas.

Electronically tagged bluefin tuna were located in the GOM ($n = 29$, Figs 1a and 2a) from December to July. Electronically tagged fish were also located in the Bahamas ($n = 6$) and northern Caribbean ($n = 1$; Fig. 1a). The mean curved fork length (CFL) of electronically tagged bluefin that entered the GOM from the North Atlantic was 241 ± 28 cm (about 11 years of age[20]). Location and diving data recorded on the tags[5,6] indicate that bluefin tuna enter the GOM along the continental slope through the Straits of Florida, diving to depths over 1,000 m (refs 5, 6), and move into the northern slope waters of the GOM. The mean SST recorded by electronic tags on bluefin tuna in the GOM (Figs 1a and 2b), inclusive of transit and aggregation periods, was 25.5 ± 1.9 °C. Electronic tag positions of bluefin tuna in the GOM, when combined with US pelagic longline observer and fisheries logbook bycatch data, identify areas of increased bluefin tuna occurrence ('hot spots') from 1992 to 2004 (Fig. 2). A majority of bluefin tuna locations (2,537 of 3,470; 73.1%) in the GOM from the three independent data sets were over the northern slope waters between the 200-m and 3,000-m contours (85° W to 95° W).

In the GOM slope waters, scientific longlining (live capture, tag and release) was conducted from pelagic longline vessels to tag giant bluefin tuna, and frequently resulted in bluefin tuna mortalities (Supplementary Table 1). This occurred even when short sets (less than 2 h soak time) and circle hooks (200 hooks or less) were used to reduce mortality. The mean size of bluefin tuna that died during capture on the longlines (237 ± 17 cm CFL, $n = 16$) was similar to the mean size of bluefin tuna captured in the GOM by commercial fishers[21]. Histological examination indicates that ovaries from mortalities in the GOM in early April (1999 and 2000) were from mature fish in pre-spawn stages. Catches sampled in mid-April or May (2000 and 2001) revealed ovaries that were well vascularized with stages that included advanced yolked oocytes, oocytes with migrating nuclei, and post-vitellogenic oocytes exhibiting atresia. These ovarian stages were indicative of ripening, final maturation and post-ovulatory oocytes[7,19,22] and are consistent with previous

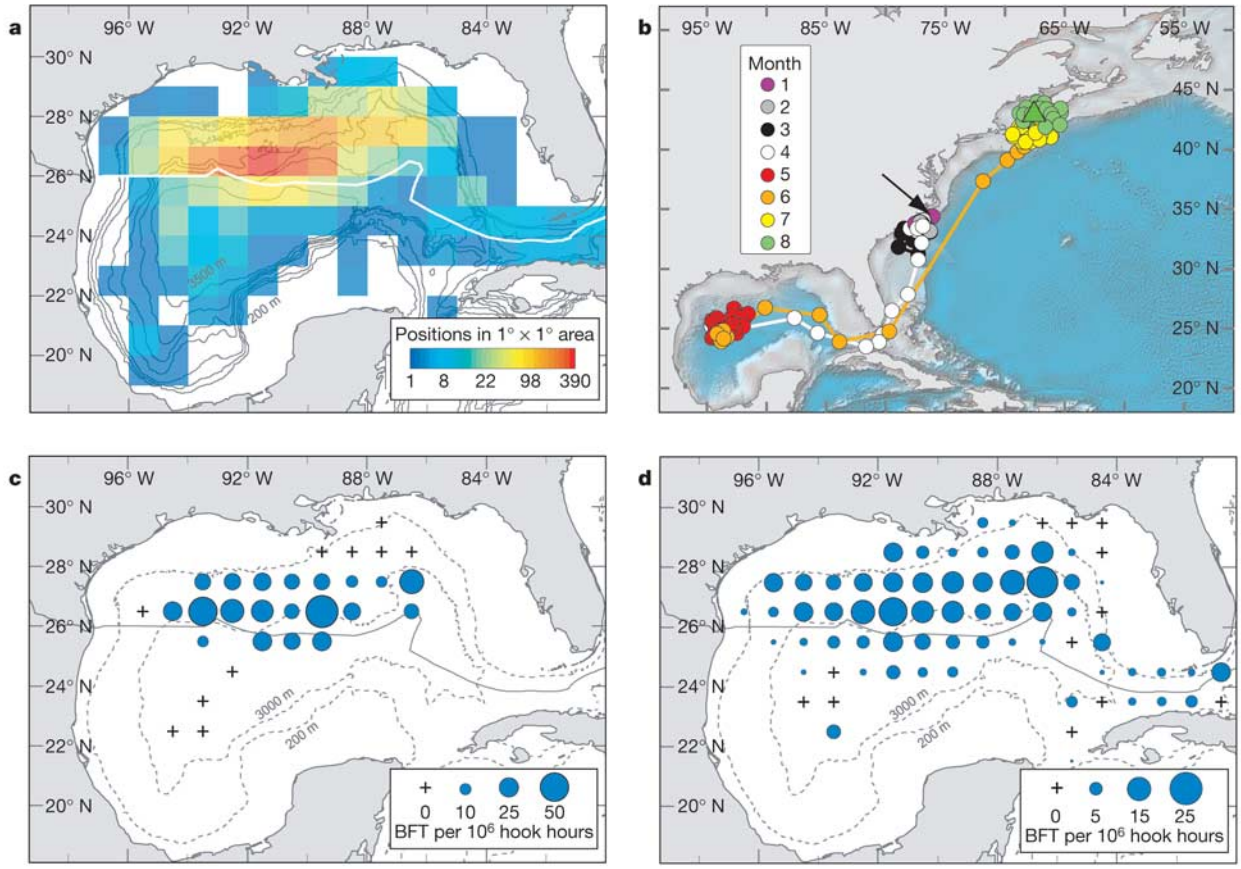

Figure 2 Occurrence of Atlantic bluefin tuna on their western spawning ground in the Gulf of Mexico. **a**, Observed locations of Atlantic bluefin tuna in the GOM based on PAT tag satellite endpoint positions and geolocation estimates from electronic tags ($n = 263$ positions, 1999–2004) and catch location statistics from pelagic longlines ($n = 3,207$, US scientific observer and US logbook data). **b**, Movements of an individual Atlantic bluefin tuna (03–251) showing a migration between the foraging grounds in the North Atlantic and the breeding grounds in the GOM. Colour denotes the month of each position. The bluefin tuna was released off North Carolina on 16 January 2004 (arrow, 268 cm CFL). The tag detached from the fish on 27 August 2004 (green triangle). **c**, Distribution of Atlantic bluefin tuna CPUE in the GOM, based on the data from the US pelagic longline scientific observer program (1992–2004). **d**, Atlantic bluefin tuna CPUE, based on US pelagic longline logbook data (1992–2003). Only 1° × 1° areas with a total effort exceeding 50,000 and 500,000 hooks are shown in **c** and **d**, respectively. Areas exceeding this minimum effort without any bluefin tuna caught are denoted by black crosses. Solid white lines (**a**) and grey lines (**c** and **d**) indicate the US Exclusive Economic Zone.

data indicating that spawning occurs in the GOM in April, May and June[10,18]. All histologically examined male testes ($n = 6$) contained spermatozoa. Recent physiological studies indicate that Atlantic and Pacific bluefin tunas have an upper thermal tolerance for cardiac Ca^{2+} uptake that is crucial for heart function[13,23] (P. Castilho and B.A.B., unpublished data). The warm waters of the GOM are favourable for the development of the eggs and larval stages but may be physiologically stressful for giant tunas, which have high rates of heat production and large metabolic demands[10]. We propose that large bluefin tuna in spawning conditions might be susceptible to mortality on longlines in the GOM because of increased thermal and hypoxic stress induced by capture in warm surface waters.

After leaving the western spawning areas, the highest density of positions of bluefin tuna occurred in the waters overlying the North American continental shelf, slope and Gulf Stream waters, the South and mid-Atlantic Bight, the Gulf of Maine and the Nova Scotia Shelf (Fig. 1 and Supplementary Fig. 1). Another region of retention occurred in the central North Atlantic in the vicinity of 40° W, east of the Flemish Cap (Fig. 1). In this area, putative western spawners become vulnerable to central Atlantic fisheries of the eastern management unit.

Bluefin tuna ($n = 26$) that had been electronically tagged in the western Atlantic showed transatlantic migrations to the Mediterranean Sea. These fish resided in the western Atlantic foraging grounds for 0.5 to 3 years before migrating to the Balearic Islands or the Tyrrhenian and/or Ionian seas (Figs 1b, 3 and 4, and Supplementary Fig. 2). These regions contain known spawning areas where mature females with hydrated oocytes, eggs and larvae have been collected[10,11,22]. Bluefin tuna were recaptured in the Straits of Gibraltar ($n = 5$) in May, potentially in transit to Mediterranean spawning areas, and in August ($n = 1$), when tuna that have spawned might be re-entering the North Atlantic. The mean size at release in the western Atlantic of bluefin tuna that were recaptured in the Mediterranean Sea ($n = 26$) was 207 ± 17 cm CFL (about 8.6 years of age[24]). Western-tagged fish recaptured in the Mediterranean Sea seem to be returning to natal spawning areas. This hypothesis implies that a proportion of bluefin tuna electronically tagged in the western Atlantic are of eastern stock origin and are affecting western fisheries.

Spawning site fidelity to the Mediterranean Sea was evident for fish that were tagged in the western Atlantic and provided multi-year records (3.3–4.6 years). Bluefin tuna 603 (191 cm CFL, released on 17 January 1999) showed one year of western residency, a transatlantic crossing to the east Atlantic (2000), and three consecutive years (2001–2003) of summer movements into and out of the Mediterranean Sea, near the Balearic Islands (Fig. 3). Bluefin 705 (222 cm CFL, released on 11 February 1999) also showed spawning site fidelity to the western Mediterranean Sea during 2000–2003 (Supplementary Fig. 2). Bluefin 408 (203 cm CFL, released on 3 March 1997) spent three years foraging in the western Atlantic before a transatlantic migration into the Ionian Sea in 2000 (ref. 5). To date, only one bluefin tuna that went into the GOM (bluefin 512, 207 cm CFL, released on 17 January 1999) had a sufficiently long track to show western spawning site fidelity over two consecutive years[5] (S.L.H.T. and B.A.B., unpublished data). Multi-year records, although rare, reveal the complex ontogeny of movement patterns, which must be accounted for in stock management.

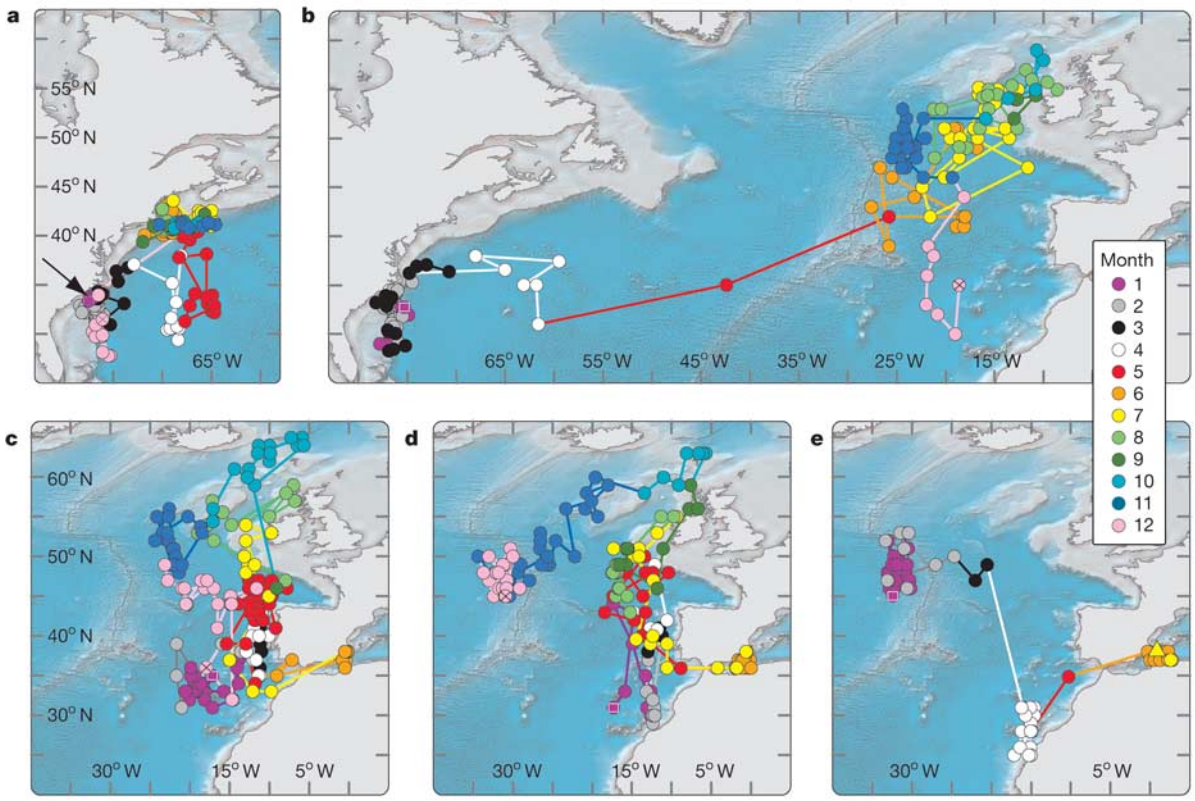

Figure 3 Movements over 4.5 years of one individual Atlantic bluefin tuna (603) that was tagged in the western Atlantic in 1999 and demonstrated site fidelity to a known spawning area in the Mediterranean Sea (2001–2003). Each panel shows a year of the fish's track; colour denotes month of each position. Start and end points for each year are denoted by a square and cross-hatched circle, respectively. **a**, The bluefin tuna was released off North Carolina on 17 January 1999 (arrow, 191 cm CFL) and showed a year of western residency. **b**, In 2000, the bluefin tuna showed transatlantic movement to the eastern Atlantic. **c**–**e**, Three consecutive years of movements from the eastern Atlantic into the Mediterranean Sea, to the vicinity of the Balearic Islands, during the breeding season: **c**, 2001; **d**, 2002; **e**, 2003. The fish was recaptured on 2 July 2003 (yellow triangle).

For fish that did not move into a known spawning ground ($n = 268$, Fig. 1c) the tracking durations were shorter (median duration 141 days) because of premature release of PAT tags or failure of sensors on early generation archival tags. We were therefore unable to discern whether, or when, these fish proceeded to breeding areas. Many fish were less than 200 cm CFL ($n = 115$) and are, by length measurements, adolescent western fish. Some bluefin tuna with an unclassified breeding status ($n = 35$, at least 200 cm CFL) did experience SSTs of 24 °C or more in the waters of the South Atlantic or mid-Atlantic Bights and Gulf Stream. Ichthyoplankton surveys in the West Atlantic have captured bluefin tuna larvae off the Carolinas, although their presence was associated with advection from the Florida Straits and not from offshore spawning[10,25]. Examination of the ovaries of the bluefin tuna captured in the winter off North Carolina ($n = 24$, 195–227 cm CFL, January to April) has so far not revealed histological evidence of spawning adults in this region. However, these areas may represent extended ranges of western spawning areas[4,5] in late spring and early summer months, and require further study.

We examined the movements of electronically tagged bluefin tuna in relation to body size and season (Fig. 4). Bluefin tuna smaller than 200 cm CFL did not enter a known ICCAT spawning area (Fig. 4a–d). Most of these fish remained west of 45° W throughout the year but displayed some range expansion in spring (Fig. 4a–d). Only bluefin tuna of larger body size (at least 200 cm CFL) occupied known spawning grounds from winter to early summer (western) and spring and summer (Mediterranean, Fig. 4e–h). This asynchrony in spawning is probably due to western spawning grounds acquiring optimal temperatures for bluefin spawning earlier than eastern spawning areas. In summer and autumn, fish of larger body size in both management units move into oceanic areas of high seasonal productivity at the northern extent of their range and along the continental shelves, while smaller bluefin remain primarily in areas along the North American shelf and slope waters (Fig. 4).

Archival tags, which have a large reward (US $1,000) to increase recovery rates, demonstrate that 32 of the 86 recaptured bluefin tuna (37.2%) moved from the western to the eastern Atlantic management unit. Inclusion of PAT tags with shorter mean track durations yields a transfer rate west to east of 14.5% (48 of 330 fish). The probability of making a west-to-east transatlantic migration in all electronically tagged fish depends on the time at liberty, putative stock origin, and body size (Supplementary Table 2). In the first 6 months after tagging, bluefin tuna from both putative stocks had a

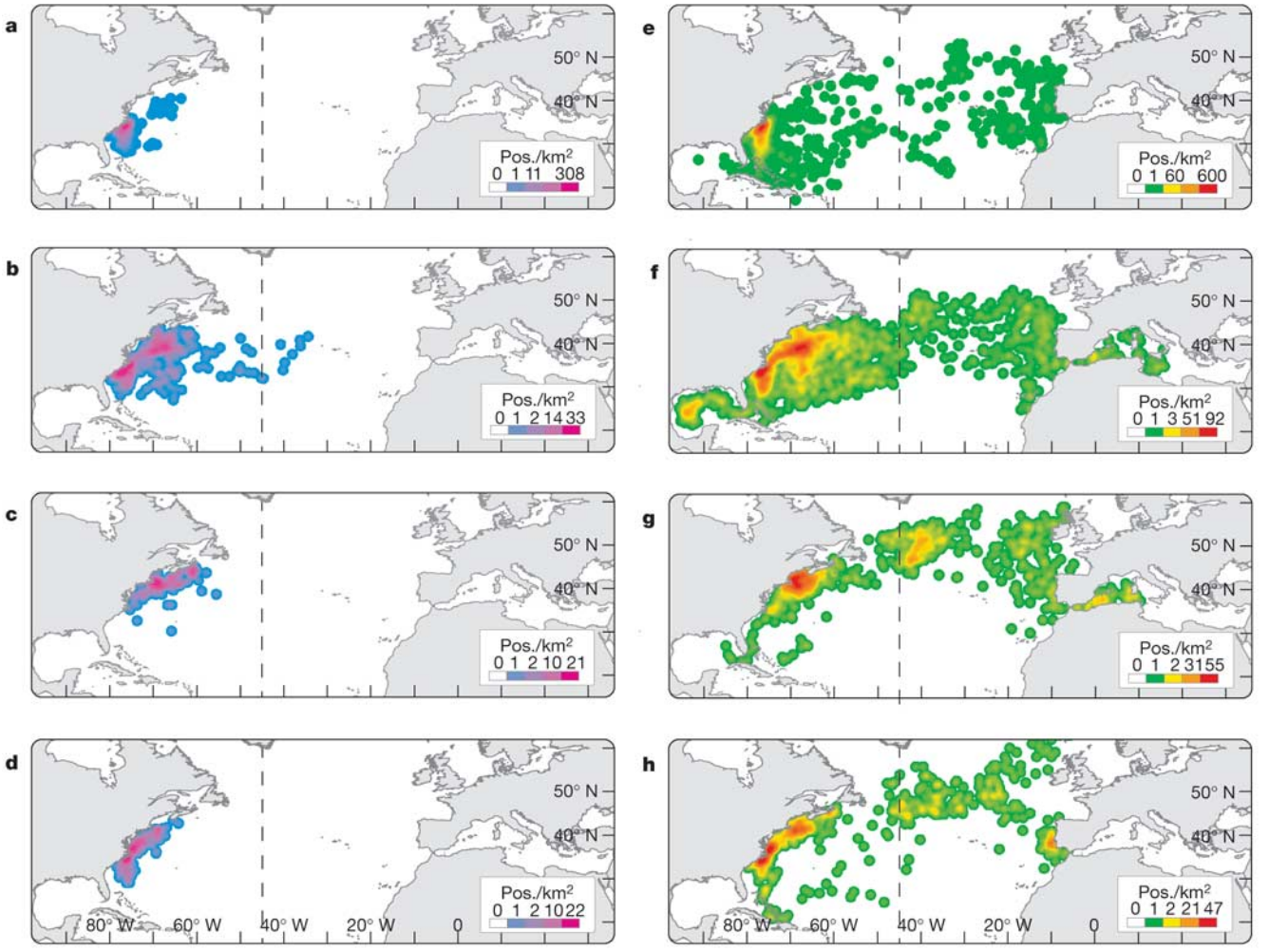

Figure 4 Seasonal distribution by size of Atlantic bluefin tuna that were tagged in the western Atlantic and measured before release. **a**–**d**, Less than 200 cm CFL. **a**, Winter; **b**, spring; **c**, summer; **d**, autumn. **e**–**h**, Greater than or equal to 200 cm CFL. **e**, Winter; **f**, spring; **g**, summer; **h**, autumn. The dashed line in each panel indicates the current ICCAT management boundary (45° W meridian). High kernel densities[29] indicate seasonal hot spots where western-tagged Atlantic bluefin tuna spent the majority of time from 1996 to 2004. Only fish that were measured were used in this analysis. A western[20] or eastern[24] growth model was applied to obtain daily length after tagging. **a**, $n = 101$, mean size at release 192 ± 9 cm CFL. **b**, $n = 56$, 192 ± 6 cm CFL. **c**, $n = 22$, 192 ± 7 cm CFL. **d**, $n = 13$, 187 ± 8 cm CFL. **e**, $n = 162$, 219 ± 14 cm CFL. **f**, $n = 167$, 220 ± 13 cm CFL. **g**, $n = 97$, 225 ± 15 cm CFL. **h**, $n = 49$, 227 ± 15 cm CFL. Pos., positions.

high probability of remaining in the western management unit (west, $0.994 > P > 0.982$; east, $0.933 > P > 0.900$; Supplementary Table 2, 95% confidence interval, 1,000 bootstrap samples). As time at liberty increases, the probability of remaining west of 45° W remains about the same for western fish but decreases rapidly for bluefin identified as eastern spawners (Supplementary Table 2). This result indicates that one component of the transatlantic migration is associated with fish of potential eastern origin moving back into the east Atlantic and Mediterranean Sea. A second component is associated with western breeding fish moving into eastern foraging grounds where encounters occur with eastern fishers (Fig. 1a).

The transatlantic movements observed in electronic tag data sets are corroborated by conventional tagging data, which demonstrate that 10% of tag recaptures from fish tagged and released in the South Atlantic Bight (1994–2000) occur in the eastern Atlantic and Mediterranean Sea[5]. Conventional tagging in the eastern Atlantic (1911–1990) indicated that 4.5% of recaptured juvenile bluefin tuna released in the eastern Atlantic were recaptured in the western Atlantic[10]. However, in these studies, no giant bluefin tuna conventionally tagged in the eastern Atlantic was recaptured in the western Atlantic[10]. Consistent with this result is the observation that no electronically tagged fish that moved into the Mediterranean Sea during spawning season has so far returned to the western Atlantic management unit. The conventional and electronic tagging data indicate that some juvenile fish tagged in the eastern Atlantic swim to the western Atlantic, where they remain for several years (Fig. 3 and Supplementary Fig. 2) before returning to Mediterranean spawning areas. We hypothesize that once an eastern spawned bluefin tuna returns from the North Atlantic to the Mediterranean it is less likely to forage along the North American coast. Fish identified as western spawners can move to the eastern Atlantic and back, crossing the 45 °W meridian several times over the course of one or more years. The overlap areas identified in the central and eastern Atlantic seem to be foraging areas for these western spawners.

Five conclusions with management implications are apparent. First, our results support the existence of two North Atlantic bluefin tuna stocks, with discrete spawning areas primarily in the GOM and the Mediterranean Sea. Second, the two stocks overlap on North Atlantic foraging grounds as adolescents and adults, but there is no evidence for movement between the two major spawning areas in the GOM and the Mediterranean Sea. Third, fish identified as western or eastern spawners are subject to fishing pressures within their designated management unit during the spawning season. Fourth, the northern slope waters of the GOM are a critical habitat for bluefin tuna during the spawning season, and these fish could be protected with time-area closures to reduce the incidental catch of giant bluefin tuna by pelagic longline fisheries operating in the GOM. Fifth, transatlantic movements of western tagged fish have two components, one associated with tuna of eastern origin moving back to the Mediterranean spawning grounds, and another with western origin fish moving into eastern Atlantic foraging grounds.

Collaborative studies that combine electronic tagging data, otolith microchemistry[26] and genetics[27] should provide a method for validating and quantifying the extent of mixing between the putative stocks. Significant questions remain, including the relationship of the two North Atlantic bluefin tuna stocks tagged in the western Atlantic to the recently identified genetically distinct stock in the eastern Mediterranean Sea[27]. Quantifying the extent of spawning in one location relative to another, establishing whether individual adult bluefin tuna spawn every year and determining the influence of physical and biological oceanographic conditions on movements are essential to improved management strategies. If the electronic tagging results are used to develop and validate new models[28] of population mixing in the context of the dynamic North Atlantic environment, ICCAT will have a better opportunity to prevent a further decline in the Atlantic Ocean's remaining bluefin tuna.

Note added in proof: During production of the manuscript, two additional tags were recaptured in December 2004 in the central Atlantic: LTD 2310 archival tag 781 at 46.49° N, 39.97° W, and LTD 2310 tag 744 at 44.50° N, 30.28° W. □

Methods

Implantable archival tags were surgically placed in Atlantic bluefin tuna from 1996 to 2004 as described previously[2,3,5,6] (Table 1). Five models of archival tags (Northwest Marine Technology v1.1 and v1.2, Wildlife Computers Mk7 versions 1 and 2, and the Lotek LTD 2310) were deployed. Specifications of the tag sensors are available at the manufacturers' websites. Fishers reported 86 archival tags with corresponding conventional external tags (Table 1), but failed to return 20 electronic tags, which were included only as deployment and recovery positions. From 1997 to 2004 (Table 1), four generations of PAT tags[5,6,9] (Wildlife Computers, hardware versions 1 and 2, with modifications) were placed externally on bluefin tuna in North Carolina ($n = 213$), Massachusetts ($n = 33$) and the GOM ($n = 27$). Pressure, light intensity, ambient and internal temperature data were recorded every 60, 120 or 128 s by the implantable archival tags. All longitude estimates were derived from light-intensity data recovered from or transmitted by the electronic tags, using threshold or template techniques[7–9]. Light-level geolocation estimates were made with manufacturers' proprietary software on-board the tag (NMT and Lotek tags) or by post-processing the data (Mk7 and PAT tags, Geocontrol v3.02 and WC-GPE Suite software). The daily SSTs were obtained from the archival tag data by extracting the ambient temperatures within 1 m of the surface[9].

Pop-up satellite archival tags collected data at intervals of 60–120 s, summarized data into 2–24-h bins, and transmitted summary data to Argos satellites (PAT software versions 1.06, 1.07, 1.08 for PAT 1.0 generation tags, 2.03 and 2.04 in 2001, 2.07a in 2002, 2.08e in 2003 and 3.01d in 2004; Wildlife Computers). SSTs and thermal profiles of the water column were obtained from the profiles of depth–temperature data transmitted by the PAT tags. These data consist of the minimum and maximum temperatures at the surface, maximum depth, and six intermediate depths, over each data summary interval. All electronic tag data were corrected for pressure drift and thermal inertia[9].

The SST data were combined with the corresponding light-level longitude estimates to obtain latitude estimates[9]. The daily maximum diving depths recorded by the tags were used to filter the geolocation estimates so that the maximum diving depth did not exceed the known bathymetry (inclusive of error estimates) at the geolocation estimate for the corresponding day. The accuracy of the geolocation estimates was validated with double-tagging experiments and by comparing the last position estimated from our algorithm with the recapture or PAT-tag endpoint positions from bluefin tuna[9]. On bluefin tuna ($n = 11$; comparisons with recapture positions), archival tags have root-mean-square (r.m.s.) errors of 0.78° and 0.90° for longitude and latitude estimates, respectively. For PAT tags ($n = 49$), the r.m.s. errors in the longitude and latitude estimates were 1.30 and 1.89°, respectively[9]. After the geolocation estimates were made, we assigned each bluefin tuna to a spawning unit: western, eastern or neutral as described above.

All fish tagged on the decks of sport fishing vessels were measured (cm curved fork length, CFL). The daily lengths of fish identified as western or eastern spawners were then calculated from the western[20] or eastern[24] growth models, respectively. The western growth model was also used for fish that were not assigned to a breeding stock. All results in this study are reported as means ± s.d. When length information is provided in the text, only fish that were measured during tagging are included.

We calculated the fixed kernel density of the positions by size class (less than 200 cm CFL and 200 cm CFL or more) and season, to make nonparametric estimates of the spatial distributions of the fish[29] (Fig. 4 and Supplementary Fig. 1). The search radius was fixed at 1.25° for all kernel density calculations because this was the mean of the geolocation errors when the data from archival and PAT tags were combined. The kernel densities were calculated with the ArcGIS 9.0 Spatial Analyst (ESRI Inc.). The seasons were delineated by the equinoxes and solstices.

The spatial overlap between the western and eastern breeders (Fig. 1) was obtained by determining the area in which both western and eastern breeders were present. We divided the study area into 1.25° × 1.25° cells and identified cells that contained geopositions from both western and eastern breeders. For both populations we calculated their 95% fixed kernel spatial distributions, with smoothing parameters estimated by least-squares cross-validation[29]. This was done with ArcView 3.3 (ESRI Inc.) and the Animal Movement Extension 2.0 (P. N. Hooge and B. Eichenlaub). The percentage spatial overlap of their spatial distributions was then calculated as a proportion of their spatial distributions[30].

The Atlantic bluefin tuna catch per unit effort (CPUE) in the GOM (Fig. 2) was calculated from data collected by the US pelagic longline scientific observer program (1992–2004) and the US pelagic longline logbook program (1992–2003). Both data sets were obtained from the US National Marine Fisheries Service. The CPUE for each 1° × 1° area was calculated if the effort in each area exceeded 50,000 and 500,000 hook hours for the observer and logbook data set, respectively. The yellowfin tuna CPUE for both data sets were also calculated for comparison (Supplementary Fig. 3).

Received 6 October 2004; accepted 17 February 2005; doi:10.1038/nature03463.

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Supplementary Information accompanies the paper on **www.nature.com/nature**.

Acknowledgements We thank R. Rinaldo, E. Prince, A. Seitz, T. Sippel, R. Schallert, N. Tulloch, G. Rosenwaks, S. Beemer, G. Shillinger, C. Perle, S. Vermillion, J. Bonaventura, D. Barber, M. Orbach, J. Jenkins, G. Stuve, P. Wright, D. Britt, B. Eakes, C. Perry, D. Brower, W. Whippen, R. Whorley, R. Jansenius, G. Sharp, R. Hill, T. Lindstrom, P. Ekstrom, P. Manuel, R. Ruais and S. Loga. We are indebted to the late Richard Novak for his contributions and sacrifice on behalf of the Tag-A-Giant programme. We thank the National Marine Fisheries Service (NMFS) for providing access to the GOM scientific observer data and US pelagic longline logbook data. The Tag-A-Giant programme was supported by grants and donations from the Packard, Pew, MacArthur, Disney, Marine Ventures, Gordon and Betty Moore, and Monterey Bay Aquarium Foundations. This research was supported in part by the NOAA NMFS, the NSF and the National Fish and Wildlife Federation. We acknowledge the extensive cooperation of the commercial and recreational captains and crews of fishing vessels in North Carolina, New England, Nova Scotia, Louisiana and Texas. We thank N. Miyabe of the National Research Institute of Far Seas Fisheries, ICCAT, A. Dinatale, G. DeMetrio, M. de la Serna and the EU COPEMED programme for return of electronic tags.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to B.A.B. (bblock@stanford.edu).

Learned kin recognition cues in a social bird

Stuart P. Sharp[1], Andrew McGowan[2], Matthew J. Wood[3] & Ben J. Hatchwell[1]

[1]*Evolution and Behaviour Group, Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK*
[2]*Marine Turtle Research Group, Centre for Ecology and Conservation, University of Exeter in Cornwall, Tremough Campus, Penryn TR10 9EZ, UK*
[3]*The Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK*

In many cooperatively breeding birds, kin selection has an important role in the evolution and maintenance of social behaviour, and 'helpers' can maximize indirect fitness gains by preferentially allocating care to close relatives[1–3]. Although there is evidence for kin-biased helping behaviour in several species[1,4,5], the mechanism of kin recognition underlying this behaviour is poorly understood[2]. Vocalizations are the most commonly used cues in avian recognition systems[6,7], but the effectiveness of vocal signals as reliable recognition cues must depend on how they are acquired[6–9]. However, there have been no experimental studies of the development of vocal recognition cues in cooperative birds; indeed, the ontogeny of all bird vocalizations other than song is poorly known in any species[10–12]. Here, we show that cooperatively breeding long-tailed tits (*Aegithalos caudatus*) can discriminate between kin and non-kin according to the individual-specific characteristics of contact calls, and show experimentally that individuals learn these calls from provisioning adults during the nestling period. Finally, we show that the pattern of cooperative behaviour in this species is consistent with the use of recognition cues learned through association.

In long-tailed tits, all adults attempt to breed independently in pairs each year, but most nests fail due to depredation[13,14]. Failed breeders often re-nest, but later in the season may instead become helpers[14]; this switch from re-nesting to helping corresponds with a seasonal change in the potential fitness benefits of each strategy[15]. No significant direct fitness benefits of helping have been found, but helpers preferentially care for close relatives[16] and accrue indirect fitness benefits by increasing brood productivity[14,15]; this kin-selected benefit represents a substantial component of inclusive fitness and is the sole source of fitness for many individuals[17]. Thus, helping is beneficial to both helpers and recipients, and selection should favour kin recognition[6,8]. Kin-biased helping occurs in the absence of reliable spatial cues to kinship[16], and a previous study suggested that long-tailed tits can discriminate between the vocalizations of close relatives and non-relatives[18]. Here, we describe an experiment that determines the characteristics of contact calls used in discrimination, and a second experiment that investigates the acquisition of these recognition cues.

Long-tailed tits have a limited vocal repertoire, with five call types and a very rarely used song[13,19,20]. The 'churr' call is a contact call given frequently by both sexes that is important for short-range communication; for example, during nest-building or aggressive interactions[13,18–20]. This call develops in the nest before fledging[20] and is highly stereotyped within individuals[21], remaining unchanged throughout adulthood (S.P.S., unpublished data); multivariate analysis showed that maximum and minimum frequency are the two most individual-specific call parameters[21]. Using a playback experiment, we tested the ability of long-tailed tits to discriminate between the churr calls of kin and non-kin according to variation in these two parameters. We conducted playback trials with four treatments at the nests of focal birds using the following