

Scent marking of key food sources in the Eurasian otter

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In the context of intraspecific competition, the distribution of key resources within a territory could influence the spatial patterns of scent deposition by territory owners, in order to maximise the defensibility of resources and reduce the costs of their defence. We investigated the pattern of spraint deposition by the Eurasian otter (*Lutra lutra*) in Mediterranean rivers of southern Italy, testing the hypothesis that spraints are concentrated around deep pools bordered by riparian vegetation because these represent important patchy sources of food. Otters strongly selected pools throughout the year, marking the largest ones which probably supported the highest fish biomass. Sprainting sites at pools were also marked more consistently than sites elsewhere on water-courses. A positive correlation between the percentage of spraints next to pools (pool markings) and overall volume of the main prey in otter diet confirmed the importance of pools as sources of prey. These results are consistent with the idea that territory owners should concentrate scent marks on key resources, as an adaptation to the constraints of defending long and narrow territories, which follow the shape of the rivers. Pool marking increased in the warm season and in December–January, but was not correlated with monthly consumption of the main prey, raising the hypothesis of an additional, reproductive function of scent marking. In the absence of specific data on reproduction or births in our study area, this hypothesis needs further investigation.

Introduction

Most mammals scent mark by depositing faeces, urine and/or the secretions of specialised skin glands on objects in their environment (Gorman & Trowbridge 1989, Hutchings & White 2000). This behaviour has often been related to territory defence (Gosling 1982, Gorman 1990), although other, not-mutually exclusive functions have been proposed, such as intra-group recognition (Gorman & Trowbridge 1989), enhancement of foraging efficiency (Kruuk 1992), signalling of either reproductive or social status or promoting

reproductive advertisement or mate attraction (Gosling & Roberts 2001a, Heymann 2006).

In the context of intraspecific competition, the abundance and distribution of resources within a territory could produce different spatial patterns of scent deposition, which aim to maximise the defensibility of limiting resources within territories and reduce the costs of their defence (Gosling & Roberts 2001b). Homogeneous and relatively small territories may be extensively marked, although with higher frequency at their periphery (Kruuk 1978, Allen *et al.* 1999, Rosell & Thomsen 2006) or along the

boundaries shared with neighbouring territories (Brashares & Arcese 1999). Large territories may be marked along inner polygons around the core area, with a number of branches extending towards the boundary, so as to maximise the chance of intercepting potential intruders (Gosling 1981, Begg *et al.* 2003, Wronski *et al.* 2006). When small social groups defend large ranges, the territory owners are forced to mark only the hinterland of their range (Gorman & Mills 1984, Balestrieri *et al.* 2011).

Eurasian otters (*Lutra lutra*) are semi-aquatic territorial carnivores following the classical model of intra-sexual territoriality showed by many mustelids (Erlinge 1967, Ó Néill *et al.* 2009). They can leave olfactory signals by both urine and the secretions of anal and ventral glands (Hutchings & White 2000), but the scent marks used most often are small, token faeces (spraints) left on prominent objects, such as large rocks (Gorman & Trowbridge 1989). Kruuk (1992) studied the pattern of spraint deposition by otters in Shetland (UK), and suggested that spraints, rather than marking the territory boundaries, were deposited to signal the use of “feeding patches”, i.e. the stretches of coast exploited by each otter for fishing.

In Mediterranean rivers, fish availability is related to the presence of isolated pools, often bordered by riparian vegetation, scattered along the river course and connected by small streams (Magalhães *et al.* 2002). Otters are primarily piscivorous (Jędrzejewska *et al.* 2001, Clavero *et al.* 2003, Remonti *et al.* 2009) and so these pools may represent important food patches (*sensu* Carr & Macdonald 1986). In southern Italy, a preliminary evaluation of the relationship between the abundance of pools and otter marking intensity revealed a positive correlation (Prigioni *et al.* 2005). To follow up this result we further investigated the marking behaviour of the otter in a freshwater habitat of southern Italy and predicted that otters would concentrate their marking activity around isolated pools. We discuss our results in relation to two hypotheses: (i) the foraging book keeping hypothesis (Henry 1977, Kruuk 1992), and (ii) the competitor assessment hypothesis (i.e. scent marks are provided to allow competitors to assess the competitive ability of

the signaller; Gosling 1981, Gosling & Roberts 2001b). In fact, in the context of the economic strategy of territorial marking (Gosling 1981), being that otter territories are generally long and thin (Green *et al.* 1984) and hardly defensible, the marking of key resources such as pools could help to reduce energetic costs to territory owners.

Most previous studies on marking behaviour in carnivores have been based on direct observations of either captive (e.g. Rostain *et al.* 2004) or free-ranging animals (e.g. Allen *et al.* 1999, Begg *et al.* 2003). This allowed the observers to gather additional information on the behaviour of signallers when marking (e.g. scratching, rolling or rubbing on the marked substrate) or on inter-sexual variation in marking intensity. However, the detailed observation of an adequate sample of otters is virtually impossible in our study area due to the low density of the otter population (Prigioni *et al.* 2006a) and the secretive behaviour of the animals. We thus used indirect techniques, particularly systematic searching for otter spraints and analysis of the spatial and temporal patterns of spraint deposition. This approach allowed regular monitoring of a wide area of the current Italian range of the species, although it involved some limitations in the data that could be collected.

Material and methods

Study area

The study was conducted along ten watercourses in southern Italy. The main hydrographic system consisted of the upper River Agri (40°20'N, 15°54'E), between the dam of Marsico Nuovo (780 m a.s.l.) and the confluence of the River Racanello (350 m a.s.l.), and its tributaries Cavolo, Alli, Casale, Sciaura, Maglia, and Racanello. We also included the neighbouring rivers Cogliandrino, Melandro and Presco, for a total of about 170 km of the river valley. Most streams are characterised by a torrential flow, the lowest discharge occurring in late summer, when waters are intensively exploited for field irrigation. The climate is Mediterranean, with rainy winters and hot dry summers. Further character-

istics of the study area have been described in detail by Smiroldo *et al.* (2009). The River Agri is part of the core of the Italian otter range and, following the progressive otter recovery which commenced at the end of the 1980s, now has a stable otter population (Prigioni *et al.* 2007).

Field survey

From March 2006 to February 2007, 22 sampling stations, each consisting of 600-m-long reaches of watercourses, were searched monthly for otter spraints. During each survey, two operators searched all of the shoreline by walking along in the shallows on both riversides (Reuther *et al.* 2000). For each sampling station, the total number of spraints found at each sprainting site was recorded, and spraints were removed for dietary analysis. Sprainting sites were identified as places with spraints separated by at least 1 m from other spraints (Kruuk *et al.* 1986).

The removal of marks did not increase spraint deposition by river otters *Lontra canadensis* (Oldham & Black 2009), while in Eurasian otters a slight increase in sprainting activity has been reported only during the first week after removal, but the increase did not occur since the second week (Brzeziński & Romanowski 2006). As our surveys were monthly, we assumed that spraint removal did not substantially alter marking behaviour in our study area.

During each monthly survey, the presence of pools (i.e. any small portion of stream at least 3 times deeper than the surrounding portion of river) along the sampling stations was recorded and their width, length and mean depth were measured. The number of pools within each sampling station varied with season, according to the hydrographic regime. The number of spraints found on the shores of each pool (i.e. those spraints found within a 2-m-wide belt around each pool) was recorded.

To test for habitat features other than pools in the 22 sampling stations, that could potentially influence otter defecation rate (Mason & MacDonald 1987), both the mean cover of bankside vegetation (CO) and mean bankside slope (SL) were estimated visually and classified into five

categories: 1 (0%–10%), 2 (10%–25%), 3 (25%–50%), 4 (50%–75%) and 5 (75%–100%).

Dietary analysis

For a random subsample of 11 sampling stations, spraints ($n = 838$) were analysed to identify the undigested remains following a standard procedure adopted in previous studies (Remonti *et al.* 2008, Smiroldo *et al.* 2009). For each faecal sample, the minimum number of individuals of each prey was estimated by the number and position (left-right) of diagnostic hard parts (e.g. mouth bones for fish, illions for amphibians). When no diagnostic part was found, the remains of prey were assigned to a single individual. The percentage volume of each food item “as ingested”, was estimated accordingly (*see* Remonti *et al.* 2008 for details). Otter diet was expressed as percentage mean volume (%mV = total estimated percentage volume of each food item as ingested/total number of examined spraints).

Data analysis

The overall and monthly percentage frequency of spraints deposited around pools (pool marking) in the 22 sampling stations was calculated with respect to the total number of spraints found in the respective periods.

The hypothesis that pools were selected by otters as marking sites was tested against the null hypothesis that spraints were uniformly distributed along the shores of the sampling stations. For this purpose, the expected number of spraints that should be found around pools if the null hypothesis was true was calculated as: [(total number of spraints found at the sampling station/total length of the two shores of the sampling station) \times total length of shores bordering the pools]. The observed and expected frequencies of pool marking were compared using a Chi-square (χ^2) test.

A random sample of 132 sprainting sites (about 20% of the total number of sprainting sites), 51 at pools and 81 not at pools, was

checked in order to estimate otter site fidelity, i.e. the frequency of monthly surveys positive for sprainting. Otter fidelity to marking sites around pool shores was compared with their fidelity towards the other sites by a Chi-square test.

The relationship between the percentage frequency of pool marking at each sampling station (i.e. the number of spraints found around pools in a sampling station/overall number of spraints found in the sampling station $\times 100$; $n = 22$) and: pool density (number of pools/100 m), pool volume ($\text{m}^3/100 \text{ m}$), mean cover of bankside vegetation and mean bankside slope was tested by a two-tailed partial correlation analysis (Johnson & Wichern 2007). This method was chosen in order to examine the relative importance of each factor to pool marking, after removing the effects of the other factors. Before the analysis, all variables were tested for normality by Kolmogorov-Smirnov's test. To achieve normality, pools marking and mean bankside slope were arcsin transformed, while pool density and volume were $\log(x + 1)$ -transformed.

A second two-tailed partial correlation was used to test the relationship between percentage pool marking and the bulk of the main food items in otter diet (%mV of fish and amphibians). Only the 11 sampling stations for which diet data were available were considered. Before this analysis, %mVs of amphibians were $\log(x + 1)$ -transformed and those of fish were x^2 -transformed.

A third two-tailed partial correlation was used to test if monthly pool marking varied

according to either fish or amphibian consumption by otters (monthly %mV).

Results

The number of pools found during each monthly survey varied from 11 to 56 (0.83–4.25 pools per km). The mean number of pools found at each sampling station was 2.1 (range: 0–6). The pools were on average 4.3-m wide, 3.9-m long and 1.7-m deep (Table 1), vs. a mean depth of the river bed of 0.3–0.5 m. A total of 1488 otter spraints were found at the sampling stations of which 604 were on the shores bordering the pools. The percentage frequency of pool marking was 40.6% vs. an expected percentage frequency, based on a uniform distribution of spraints, of 2.9% ($\chi^2 = 7399$, $\text{df} = 1$, $p < 0.001$).

Otters marked the largest pools most intensively, irrespective of pool density; pool marking was not influenced by bankside vegetation cover or slope (Table 2). Otters showed higher fidelity to the marking sites located around pools (Table 3).

Fish (%mV = 50.5) and amphibians (%mV = 40.0) formed the bulk of the otter diet; the other food items (reptiles, crustaceans, mammals) represented less than 5% each of the diet. A positive correlation was found between the annual frequency of pool marking and the %mV of fish (Table 2).

Otters strongly selected the pools for marking throughout the year (Fig. 1), with a main peak in the warm season and a second peak in December–January ($\chi^2 = 317$, $\text{df} = 11$, $p < 0.001$). However, no relationship emerged between monthly pool marking and the %mV of the main prey of otters (Table 2).

Table 1. The number and mean size (m) of the pools found during each monthly survey.

Month	Number of pools	Mean width	Mean length	Mean depth
January	37	4.3	4.0	2.0
February	18	4.4	4.1	2.0
March	11	4.4	4.7	1.8
April	29	4.1	3.9	1.8
May	46	4.7	3.8	1.8
June	49	4.5	3.7	1.8
July	51	4.3	3.5	1.7
August	51	4.3	3.5	1.6
September	56	4.1	3.5	1.5
October	53	4.2	3.6	1.6
November	56	4.3	3.8	1.6
December	43	4.4	4.1	1.7

Discussion

The pattern of spraint distribution found in our study area provides evidence that otters were scent marking patchily distributed sources of their main prey. Pools were intensively marked throughout the year and marking increased with pool size, which is known to be positively related to fish biomass (Elso & Giller 2001, Stichert *et al.* 2001, Harvey *et al.* 2005, Warren

et al. 2010, Whiteway *et al.* 2010). Accordingly, annual marking intensity was correlated with otter consumption of their main prey, confirming the importance of pools as sources of food. Finally, other environmental factors, such as vegetation cover and river bank slope, did not influence the distribution of spraints.

A relationship between marking behaviour and the signalling of key resources has previously been reported for otters living on the coasts of Shetland (Kruuk 1992). There, spraints were mainly deposited by otters landing just before or after a fishing bout. Moreover, a high percentage of spraints was deposited in the intertidal zone or close to the low tide level, suggesting a communicative function limited to a short period of time. Kruuk hypothesized that scent marking allows otters to signal to their conspecifics food patches that had already been exploited, thus maximising their feeding success by avoiding depleted sections of the coast. Conversely, he did not find evidence of spraint deposition near range boundaries, suggesting a minor role of spraints in territorial defence. Sillero-Zubiri and Macdonald (1998) described a similar pattern of scent marking for Ethiopian wolves (*Canis simensis*), which, living in social

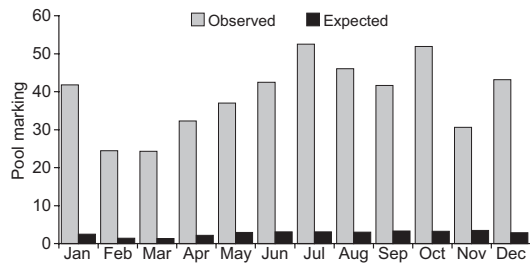


Fig. 1. Observed and expected monthly pool marking (percentage of spraints found within 2 m from pool shores) by Eurasian otters (*Lutra lutra*) in southern Italy.

groups but hunting alone, reduced competition for undisturbed foraging patches by signalling to pack companions the areas that had recently been hunted.

From an evolutionary point of view, the function of a signal has to be interpreted in relation to its benefits for the signaller. A pattern of scent communication which includes benefits for individuals other than the signaller entails some form of cooperative behaviour, which may compensate for the costs of altruistic acts (Novak 2006). While in Shetland up to four adult females share group ranges (Kruuk & Moorhouse 1991), in freshwater ecosystems each adult female and

Table 2. Partial correlation analyses between: (i) annual pool marking (APM) by otters *Lutra lutra* and volume of pools ($\text{m}^3/100 \text{ m}$), density of pools (number of pools/100 m), mean cover of bankside vegetation (CO) and mean bankside slope (SL); (ii) annual pool marking and annual %mV of fish (AVF) or amphibians (AVA) in otter diet; (iii) monthly pool marking (MPM) and monthly %mV of fish (MVF) or amphibians (MVA) in the otter diet.

Tested variables	Control variable	<i>r</i>	df	<i>p</i>
APM vs. pools volume	Pools density	0.57	19	0.006
APM vs. pools density	Pools volume	-0.23	19	0.31
APM vs. CO	SL	0.10	19	0.67
APM vs. SL	CO	-0.14	19	0.54
APM vs. AVF	AVA	0.69	9	0.019
APM vs. AVA	AVF	0.49	9	0.13
MPM vs. MVF	MVA	-0.12	9	0.75
MPM vs. MVA	MVF	-0.42	9	0.23

Table 3. Comparison between otter *Lutra lutra* fidelity to marking sites at pools (within 2 m from their borders) and not at pools (see methods).

	Number of surveys	Number of positive surveys	Site fidelity	χ^2	df	<i>p</i>
Sites at pools	396	185	46.7	27.8	1	< 0.001
Sites not at pools	575	173	30.1			

its offspring occupy exclusive territories, overlapped by the larger territories of adult males (Erlinge 1967, Ó Néill *et al.* 2009). Thereby, a stretch of river is expected to be shared by two resident, unrelated adults (one male and one female). If it were confirmed for freshwater habitats, the mechanism of scent communication hypothesized by Kruuk (1992) should be based on direct reciprocity, relying on repeated encounters between the two individuals that lead to cooperative behaviour in the framework of the iterated Prisoner's Dilemma (Axelrod & Hamilton 1981).

An alternative function of scent marking which does not require cooperative behaviours is related to territory defence, with scent marks acting as signposts towards potential intruders. The basis of this system may be that residents signal ownership to intruders and reduce the costs of territoriality when intruders withdraw to avoid costly encounters, a form of competitor assessment (Gosling 1982). In freshwater habitats otter territories generally follow the shape of river banks and so are less economically defensible than those with a lower perimeter-to-surface ratio. As an example, in Ireland, adult otter territories cover from 5.9–10.4 km of river for females to 7–17.4 km for males (Ó Néill *et al.* 2009); male ranges along ca. 50 km of river have also been reported (Durbin 1996). In river basins neighbouring our study area, the genetic typing of fresh faeces revealed the stable presence of single individuals up to 34.8 km of watercourses (Prigioni *et al.* 2006b). Continual patrolling and marking of the boundaries of such long and narrow territories would involve high costs, so otters may be forced to concentrate their marks next to inner key locations, where the chance of intercepting and deterring an intruder from exploiting them is the highest (Gosling 1981). Contrary to the situation reported by Kruuk (1992) for coastal areas, spraints may persist on river shores for long periods, although their persistence and the efficacy of their communicative function are influenced by climatic and flood conditions. For example, Brzeziński and Romanowski (2006) reported the disappearance of 7.7% of spraints in 20–30 days, while Jenkins and Burrows (1980) concluded that 50% of spraints vanish within two weeks after deposition.

In our study area, otter marking behaviour suggested a stable and widespread preference for pools, which is consistent with an emphasis on scent marking of key resources in the context of intra-specific resource defence. To confirm this hypothesis, further studies should address the socio-biology and territorial behaviour of otters in southern Italy.

Regarding the mechanism involved in scent communication, further studies based on direct observations of the behaviour of both signalers and receivers are needed. Some predictions of the “scent matching” hypothesis (Gosling 1982) have yet to be confirmed. For example, although otters are able to distinguish between their own and others' spraints (Rozhnov & Rogoschik 1994) overmarking has been reported only occasionally (Durbin 1989, Brzeziński & Romanowski 2006, Oldham & Black 2009).

Monthly variation in pool marking and the lack of a significant relation with the corresponding rate of consumption of the main prey could raise the hypothesis of an additional function of scent marking, not related to territoriality. Seasonal changes in marking rate could be related to the signalling of the reproductive status of the individuals (Gorman & Trowbridge 1989). River otters are able to discriminate the sex of conspecifics from the scent of spraints (Rostain *et al.* 2004), although urine may be more important than faeces in the communication of reproductive status and oestrous condition (Gorman & Trowbridge 1989). Alternatively, in captive otters, peaks of marking activity have been reported to occur when cubs are 5–6 months old and start to move within the family group territory (Prigioni *et al.* 1995). Nevertheless, free ranging otters do not show clear seasonality in reproduction, which makes it difficult to predict corresponding peaks in marking activity. Birth peaks have been reported in summer and autumn in Norway, (Heggberget & Christensen 1994), in March–June in Pre-Pyrenees rivers and in December–January in Mediterranean Spain, although births can occur throughout the year and their time can be influenced by variation in food availability (Ruiz-Olmo *et al.* 2002). Data on reproduction or births in our study area are lacking, so the hypothesis of a relationship between scent communication and reproductive cycle could not be tested.

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