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Non-intrusive monitoring of otters (*Lutra lutra*) using infrared technology

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Abstract

Remote, non-intrusive monitoring of elusive mammals remains problematic, particularly in running waters. The utility of using submerged infrared counters for monitoring non-intrusively the activity of Eurasian otters *Lutra lutra* was assessed in three tributaries of the River Dee (Beltie, Cattie, Feardar; Scotland) during 2003–2004. Otters passing through the infrared counters were strongly nocturnal and displayed a bimodal diel activity pattern. Seasonal activity indices varied fourfold between tributaries and peaked during the salmonid breeding season. The median time elapsing between consecutive night visits was 2.02 ± 0.79 days and did not differ between tributaries. The median head–body length of adult otters was estimated at 75.0 ± 1.1 cm, whereas median upstream swimming speed was calculated at $0.97 \pm 0.01\,\mathrm{m\,s^{-1}}$. Minimum census estimates revealed the activity of at least two adults in the Beltie, two adults and three juveniles in the Cattie, and two adults with one juvenile in the Feardar. Our study indicates that, under suitable conditions, infrared technology can be used effectively to examine non-intrusively the activity of free-ranging otters in running waters, offering some advantages over previous, more intrusive techniques that relied on the collection of spraints, the use of radioisotopes or the tracking of marked individuals.

Introduction

Increasingly, one of the greatest challenges in wildlife conservation is monitoring endangered or elusive species in the field without disturbing them (Stearns & Stearns, 1999; Mace *et al.*, 2001). Techniques for wildlife monitoring are legion (Wilson & Delahay, 2001) and often include intrusive methods such as mark and recapture (Banks *et al.*, 2005), as well as more passive monitoring methods such as thermal imaging (Gill, Thomas & Stocker, 1997), fur identification (Belant, 2003), individual voice recognition (Terry & McGregor, 2002) or DNA analyses from faecal or fur samples (Dallas *et al.*, 2003). Every technique has its limitations (e.g. Wilson & Delahay, 2001; Davison *et al.*, 2002), and elusive and trap-shy species have proved particularly difficult to monitor (Karanth & Nichols, 1998).

Real-time, time-lapse and animal-triggered image-capture technologies are increasingly being used in ecological studies of vertebrates (Cutler & Swann, 1999). These non-intrusive, image-capture technologies often rely on using phenotypically and morphologically distinct features to identify individuals or species (e.g. body size and shape, coloration, facial patterns and scarring) and have proved to be extremely useful as demographic and population monitoring tools for a variety of high profile but elusive species. Advances in terrestrial camera-trap systems have greatly facilitated the study of nocturnal and rare carnivores, such as the tiger *Panthera tigris* (Karanth *et al.*, 2004) or the jaguar *Panthera onca* (Silver *et al.*, 2004), but non-intrusive monitoring of aquatic vertebrates poses additional problems. Image capture–recapture techniques have been used to study the distribution and social system of marine mammals (Coakes *et al.*, 2005; Karczmarski *et al.*, 2005), but no satisfactory camera trap has yet been developed that works well underwater at night or in running waters. Consequently, the nocturnal behaviour of many aquatic vertebrates, including most riparian mammals, remains poorly known (Gorman *et al.*, 1998; Sutherland, 2002).

The Eurasian otter *Lutra lutra* provides an example of a protected mammal whose patterns of activity remain unclear, despite considerable investment of resources. This active, semi-aquatic fish predator is extremely trap shy and has a strong aversion to human disturbance (Kruuk, 1995). It also undertakes extensive nocturnal forages over a wide geographical area (Chanin, 1985), which makes direct observations difficult, especially in running waters (Mason & Macdonald, 1986). Terrestrial image-capture cameras used to monitor marten or mink activity appear unable to detect the presence of otters (Jones & Raphael, 1993; González-Esteban, Villate & Irizar, 2004), presumably because otters forage and travel predominantly through the water. Not surprisingly, information on the demography, abundance and activity patterns of wild, free-ranging otters in streams is scant (Gorman *et al*., 1998; Kruuk *et al*., 1998). This is unfortunate because the otter is a protected, flagship species throughout its range (Mason & Macdonald, 1986; Kruuk, 1995).

Patterns of otter activity and abundance have traditionally been inferred from field surveys of holts (Kruuk *et al*., 1989) or spraints (Kruuk *et al*., 1986; Strachan & Jefferies, 1996), from snow tracking (Sidorovich, 1991), from mark and recapture with radioisotopes (Kruuk, Gorman & Parish, 1980), from telemetry studies (Green, Green & Jefferies, 1984; Ruiz-Olmo, Jiménez & López-Martín, 1995; Beja, 1996), or from direct observations of wild or captive animals during limited periods (Kruuk, 1995). None of these methods are without shortcomings (Romanowski & Brzezinski, 1997; Ruiz-Olmo, Saavedra & Jiménez, 2001), and consequently many aspects of otter ecology remain poorly known (Chanin, 1985; Kruuk, 1995). Moreover, some methods such as the use of radio-labelled isotopes or the fitting of radio-transmitters may no longer be acceptable. Indeed, a question remains as to the validity of conclusions from mammalian studies that impose stress upon individuals or interfere with their normal behaviour.

Here we report on an assessment of a novel, non-intrusive image-capture technique to examine the activity of otters and other aquatic vertebrates in the field with the aid of a submerged infrared beam counter. We present real-time data on diel and seasonal activity patterns of otters in three tributaries of the River Dee (Scotland), and derive information on body size and swimming speeds of otters foraging in the wild. We also present a conservative estimate of otter numbers based, for the first time, on actual counts of individuals passing simultaneously through each tributary.

Methods and materials

Study sites

The study was conducted between September 2003 and March 2004 in three second-order tributaries of the River Dee (Aberdeenshire, Scotland): the Beltie, the Cattie and the Feardar burns (Fig. 1). The burns support natural populations of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* (both resident and migratory), as well as European eels *Anguilla anguilla* and minnows *Phoxinus phoxinus*. Otters are abundant throughout the Dee watershed but tend to use the small tributaries predominantly during the autumn, coinciding with the spawning migrations of salmonids (Carss, Kruuk & Conroy, 1990). Feral American mink *Mustela vison* are also found in the Dee tributaries (Jenkins & Harper, 1980; Carss *et al*., 1990).

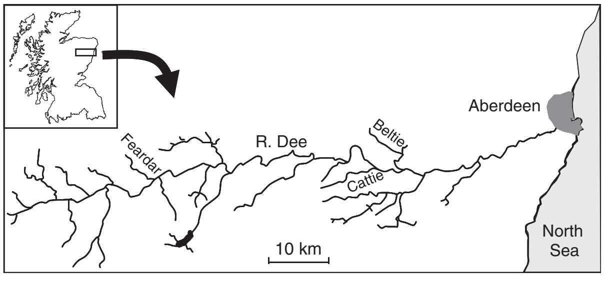

Figure 1 Location of the three tributaries of study in the River Dee watershed (Scotland).

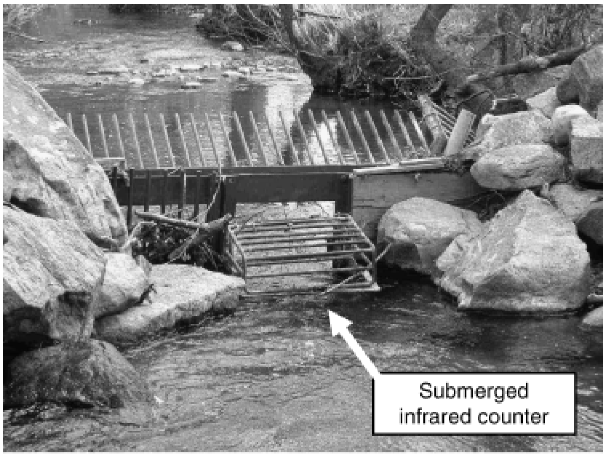

Figure 2 The Cattie Burn, showing counting fence and location of the submerged infrared counter in the exit gate (photograph Tony Hawkins).

Infrared counters

One 'Vaki Riverwatcher' fish counter (Vaki Aquaculture Systems Ltd, Kópavogur, Iceland) was deployed in each tributary near their respective confluences with the River Dee (Fig. 2). The counters operated almost continuously from September 2003 to March 2004 in the Beltie and the Cattie, and from November 2003 to March 2004 in the Feardar (Table 1). Vaki counters use two arrays of submerged photocells and a scanner to produce an infrared beam between two plates (20 cm wide × 60 cm high, gap 10–45 cm). This arrangement allows the generation and storage of two silhouette images each time the infrared beam is interrupted by a passing object. Proprietary software allows operators to select the minimum size of objects the scanner records and thus allows some degree of filtering of unwanted noise. Each silhouette image generated by the counter, however, needs to be screened and verified by an observer. A description and accuracy of the Vaki counter for counting salmonids is given in Shardlow & Hyatt (2004) and the Vaki user manuals (downloadable from www.vaki.is).

Water temperature was recorded automatically every 3 h by sensors fitted to the counters and varied from 0 to 11.3 °C in the Beltie, from 0 to 13.0 °C in the Cattie and from 0 to 6.7 °C in the Feardar. The counter deployed in the Beltie incorporated an underwater video camera, which was used to verify the identity of the silhouette images (most of which were of adult salmon and trout).

Estimates of otter body size (head–rump length in cm) were calculated from the maximum heights (h) of the stored otter silhouettes (see Fig. 3). We used a 6.15 ratio between

Table 1 Estimates of otter *Lutra lutra* activity in three tributaries of the River Dee (Scotland) derived from crossings through submerged infrared counters

Tributary	Period of study	Number of observation nights[a]	Total number of otter crossings (≥59 cm)	Average number of otter crossings per night ± 95 CI	Daily mean temperature (min–max) (°C)
Beltie	4 Sep 2003–18 Mar 2004	197	47	0.24 ± 0.09	0.0–11.3
Cattie	4 Sep 2003–19 Mar 2004	171	138	0.81 ± 0.22	0.0–13.0
Feardar	10 Nov 2003–10 Mar 2004	125	25	0.20 ± 0.10	0.0–6.7

[a] Excluding nights without data because of system malfunction (Beltie = 0, Cattie = 22, Feardar = 5).

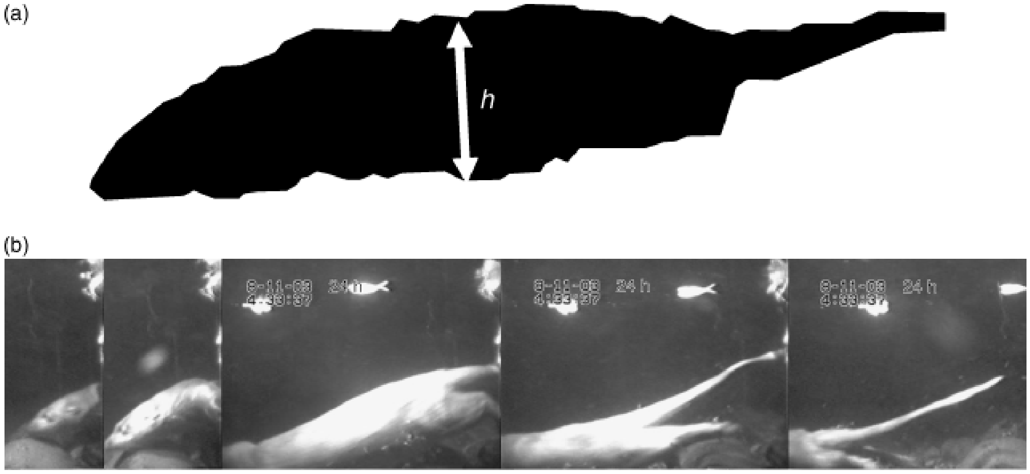

Figure 3 (a) Silhouette of an otter *Lutra lutra* passing through the Beltie infrared counter at 04:33 h on 8 November 2003 showing the metric used to estimate maximum body height (*h*) and (b) still images of the same animal exiting the infrared counter, as captured by the underwater camera.

body height and head–rump length derived from infrared otter silhouettes, underwater images of otters exiting the Beltie counter and published data on Eurasian otter biometrics (shoulder height minus foreleg size; Macdonald & Barrett, 1993). As body height is less affected than body length by the undulating motion of animals swimming through the counter, maximum height is the preferred metric for estimating body size from stored Vaki silhouettes (Shardlow & Hyatt, 2004). Upstream swimming speeds ($\mathrm{m\,s^{-1}}$) of otters passing through the counter photocells were calculated automatically by the Vaki software. These are swimming velocities over the ground, as otters (with one exception) were always recorded swimming against the current.

Concordance and validation of results

We used an underwater video camera in the Beltie to match otter images to infrared otter silhouettes and to derive preliminary rules for identifying otters from fish and spurious signals. We then carried out a double-blind test to assess the concordance of results. A total of 5484 infrared signals was given to three observers (S. D., C. G. L. and D. W. F.) working independently, who were asked to identify those signals belonging to otters.

To reduce the risk of wrongly classifying American mink silhouettes as otters, we excluded all silhouettes of animals with a head–tail size of less than 59 cm (the maximum head–tail length of American mink; Chanin, 1985; Macdonald & Barrett, 1993). If an adult otter (>59 cm) was identified along with an almost simultaneous record (within 1 min) of a smaller individual (<59 cm), we took this to indicate the passage of adult(s) and young. We acknowledge that this cut-off point may have excluded some juvenile otters from being recorded, but consider this size restriction to provide a conservative estimate of otter passages through the counters.

Minimum census estimates

Minimum census counts of the number of otters active during the period of study were estimated by taking into account the body size and simultaneous passage of otters through the counters in each tributary. We assumed that upstream otter silhouettes recorded within 1 min of each other were most likely to have been caused by the passage of several individuals passing independently through the counters. We also assumed that otter silhouettes differing by more than 20 cm in body size belonged to different individuals.

Results

Identification of otters from infrared silhouettes

The Beltie counter generated a total of 721 infrared silhouettes that were classified as fish (mostly spawners of Atlantic salmon and brown trout), 50 silhouettes that were classified as adult otters (59 cm), and three silhouettes that were classified as juvenile otters or mink (<59 cm). Agreement in identifying adult otter silhouettes from other signals by three observers working independently was 99.8%, and the proportions of otter silhouettes identified by each observer were similar (55, 50 and 62; $G = 1.00$, d.f. = 2, $P = 0.61$). Otter silhouettes (Fig. 3) were normally easily recognized from fish images (Fig. 4) by having a distinctive trailing tail, absence of fins and a characteristic body shape with a downward-pointing head. Fully grown adult otters ($n = 210$) were also clearly recognized from potential mink silhouettes ($n = 17$) by their much larger body size.

Diel and seasonal activity patterns

The diel activity of otters, as measured by the number of crossings through the counters grouped in 4 h intervals, was clearly non-random in all tributaries (Beltie: $\chi^2 = 38.40$, d.f. = 5, $P<0.0001$; Cattie: $\chi^2 = 82.00$, d.f. = 5, $P<0.0001$; Feardar: $\chi^2 = 24.68$, d.f. = 5, $P<0.0001$). Otters were strongly nocturnal and few or no otters were recorded after 07:00 h or before 17:00 h GMT (Fig. 5). There was no difference in diel activity between tributaries ($G = 1.79$, d.f. = 10, $P = 0.99$), and two peaks of activity were evident, one occurring just before dawn (between 04:00 and 06:00 h) and one occurring in the middle of the night (between 21:00 and 23:00 h) (Fig. 5).

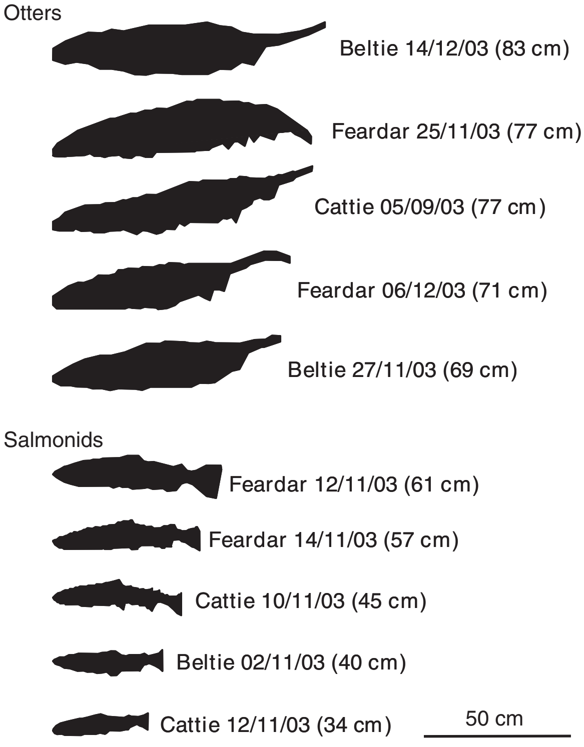

Figure 4 Sample infrared silhouettes of otters *Lutra lutra* and salmonids passing through the submerged counters deployed in three tributaries of the River Dee during 2003–2004.

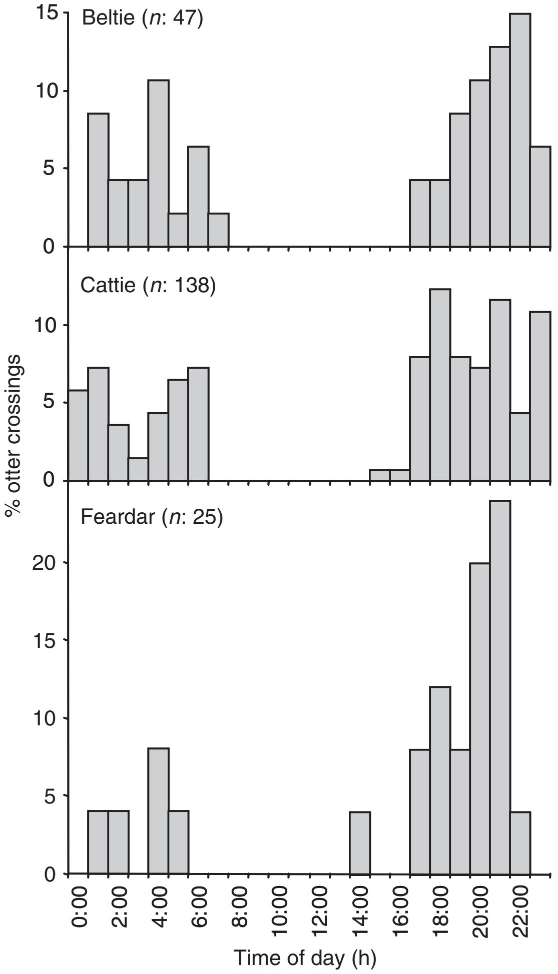

Figure 5 Diel activity patterns of otters *Lutra lutra* in three tributaries of the River Dee based on the number of crossings through the infrared fish counters during September 2003–February 2004.

Analysis of nightly activity patterns (Fig. 6) grouped at monthly intervals indicated a strong, non-random seasonal trend in the three tributaries (Beltie: $\chi^2 = 52.07$, d.f. = 6, $P<0.0001$; Cattie: $\chi^2 = 40.26$, d.f. = 6, $P<0.0001$; Feardar: $\chi^2 = 38.38$, d.f. = 4, $P<0.0001$), as the activity of otters seemed to peak during the salmonid breeding season. Serial analysis revealed a significant non-random pattern of nightly visits in the rivers Beltie and Feardar (Wald–Wolfowitz runs test, Beltie, $P = 0.007$; Feardar, $P<0.0001$), but not in the river Cattie ($P = 0.37$), which was the most frequently visited. The time elapsing between visits by otters was very similar and not significantly different between tributaries (Fig. 7; Kruskal–Wallis, $P = 0.396$). The median

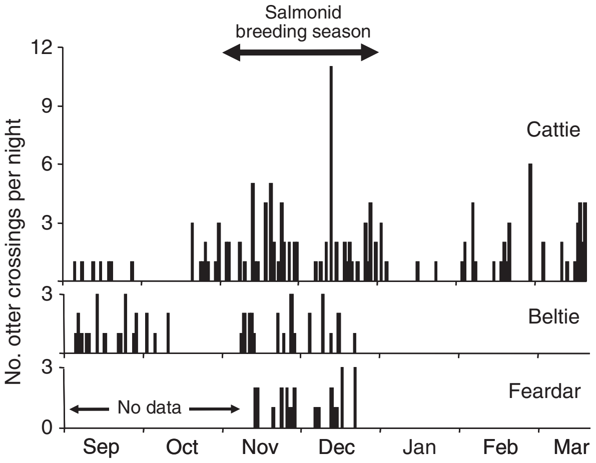

Figure 6 Seasonal activity patterns of otters *Lutra lutra* in the Beltie, Cattie and Feardar burns during September 2003–March 2004 based on the number of nightly crossings through the infrared fish counters.

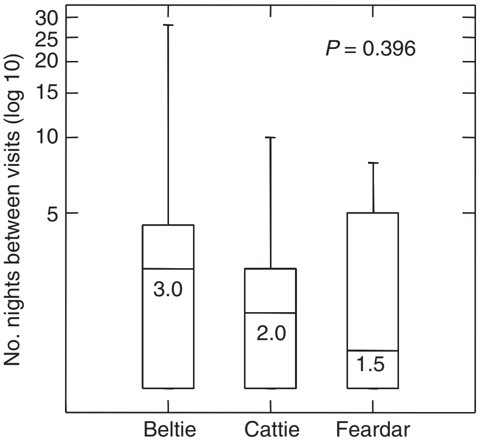

Figure 7 Number of nights elapsing between consecutive night crossings by otters *Lutra lutra* in three tributaries of the River Dee; numbers inside the boxplots denote median values, whereas probability refers to the results of a non-parametric analysis of variance.

elapsing time between consecutive night visits was 2.02 days [95% confidence interval (CI) = 1.24–2.81].

Estimates of otter body size and swimming speed

Estimates of body size (head to rump length) based on measurements of silhouette heights converted to body sizes indicated that there were no significant differences between tributaries (Fig. 8a; Kruskal–Wallis, $P = 0.057$). The median otter body size was 75.0 ± 1.1 cm for the three tributaries. Otters were recorded swimming upstream through the counters at a median speed of 0.93–1.19 m s^{-1}, although the range was quite variable (0.09–4.28 m s^{-1}; Fig. 8b), probably reflecting the varying flow conditions in the river (Fig. 8b). The median upstream swimming speed was 0.97 ± 0.01 m s^{-1}.

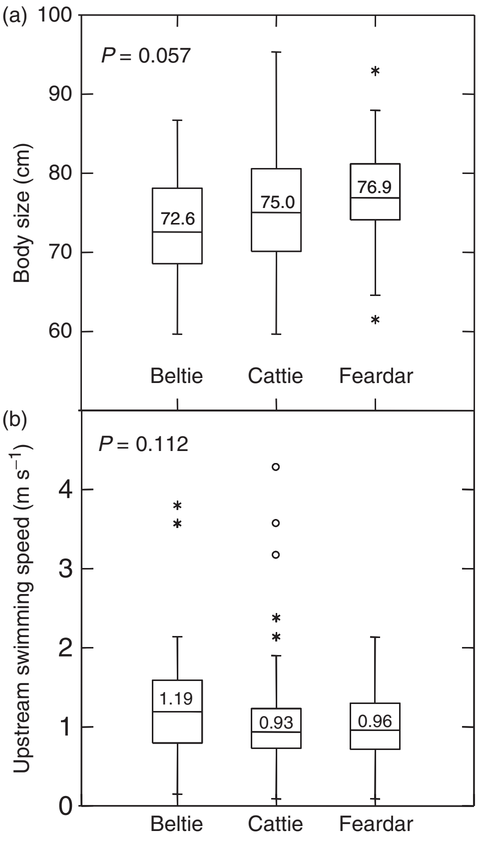

Figure 8 Estimates of (a) body size (without tail) and (b) upstream swimming velocity of otters *Lutra lutra* passing through the infrared counters in the three tributaries of the River Dee. Numbers inside the boxplots denote median values, whereas probabilities refer to the results of a non-parametric analysis of variance.

Minimum census estimates

Census estimates of the number of active otters during the period of study were two adults (71–81 cm) in the Beltie, two adults (81–93 cm) and three juveniles (58–64 cm) in the Cattie, and two adults (72–90 cm) with one juvenile (55 cm) in the Feardar. These are minimum estimates based on the near-simultaneous passage of different individuals through the three counters.

Discussion

This study is the first to demonstrate the utility of submerged infrared counters, originally devised for counting fish at hatcheries, for remotely monitoring the activity of elusive riparian mammals such as the Eurasian otter under natural river conditions. With proper calibration, infrared counters can also provide novel data on body size and swimming speeds of wild otters with minimum or no interference, a matter of increasing concern with protected species. Although infrared counters alone cannot discriminate between individuals, and thus may be recording the same individual on several occasions (thus leading to pseudo-replication; cf. Heffner, Butler & Reilly, 1996), this is a problem common to most other survey methods (Ruiz-Olmo *et al.*, 2001). Likewise, the extent to which otters can bypass infrared counters (thus avoiding detection) is not known, although work is currently underway to address this issue. It is possible that the use of infrared counters with high-resolution cameras (such as the one installed on the Beltie) may allow for the unique identification of at least some individuals. It is also likely that the use of infrared counter technology, perhaps in combination with other non-intrusive techniques such as genetic analysis of faecal samples (e.g. Dallas *et al.*, 2003), will help to better assess the conservation status and distribution of otters and other riparian mammals (e.g. Strachan & Jefferies, 1996).

The seasonal activity of otters in this study appears very similar to results derived from the intensity of sprainting for otters living in other Scottish streams, with activity typically peaking in late autumn and early winter and decreasing thereafter (Kruuk, 1995). Otters in the three Dee tributaries displayed strong nocturnal behaviour, as reported for other small salmonid streams (e.g. Chanin, 1985; Mason & Macdonald, 1986), but in sharp contrast to otters inhabiting coastal waters which tend to forage mostly during the day (Kruuk, 1995). Some authors have noted a strong seasonal dependence of Scottish otters on salmonids, which appears to peak during the autumn (Mason & Macdonald, 1986; Kruuk, 1995) when salmonid spawners may be particularly vulnerable. Indeed, Carss *et al.* (1990) noted that otters often preyed on large adult salmon during the spawning season, something they seldom did at other times of the year. However, the extent to which the exploitation by otters of small tributaries is timed seasonally to match the upstream migrations of salmonids in the autumn is not clear. Our preliminary results suggest that there was an increase in otter activity coinciding with the annual spawning migrations of salmonids, but whether these were causally linked awaits further investigation.

Activity indices, measured as the average number of otter crossings through the counters per night, varied fourfold in our study, although the median time elapsing between night visits (2.02 days) was not different between tributaries. This suggests that otters may have been adjusting the frequency and length of their foraging excursions differently between tributaries, perhaps in response to differences in prey availability or otter population density. In this respect, by providing simultaneous information on the passage of both prey and predator, infrared counters have the potential for providing a useful insight into prey–predator interactions, an issue of increasing concern for reducing the conflict between piscivorous predators and fisheries (e.g. Wires *et al.*, 2003).

Estimates of head to body length derived from infrared silhouettes (60–85 cm) were not far from the typical range found for this species (males: 60–90 cm; females: 59–70 cm; Macdonald & Barrett, 1993), suggesting that infrared counters can also provide reasonably accurate morphometric data. There are very few measurements of swimming speeds and associated energetic costs of otters in running waters (Ruiz-Olmo *et al.*, 1995; Kruuk & Carss, 1998), although Nolet, Wansink & Kruuk (1993) recorded swimming speeds of 0.26–1.5 $\mathrm{m\,s^{-1}}$ while fully submerged. In an artificial swimming channel, Eurasian otters averaged a swimming speed of 0.89 $\mathrm{m\,s^{-1}}$, although the energetic cost of swimming at 1.3 $\mathrm{m\,s^{-1}}$ was also minimal, amounting to 0.95 $\mathrm{J\,N^{-1}\,m^{-1}}$ (Pfeiffer & Culik, 1998). These values are strikingly similar to the estimated median swimming speed of $0.97 \pm 0.01\,\mathrm{m\,s^{-1}}$ recorded in our study, suggesting that infrared counters can be used to derive reasonable estimates of otter swimming speeds under field conditions.

Potential applications

The use of infrared counters has potentially a number of important applications for ecological research and the conservation of riparian mammals. For example, by installing a network of counters within a river catchment, it is possible that the size, range and demography of specific otter populations could be assessed with some degree of accuracy. Our preliminary data, based on the near-simultaneous passage of otters through three separate tributaries, are consistent with the existence of at least two adults in the Beltie, two adults and three juveniles in the Cattie, and two adults and one juvenile in the Feardar. However, the extent to which these represent different populations is not clear. Refinements to existing image-capture systems might provide further opportunities for individual identification or gender assignment of fully grown adults based on physical characteristics (otters are strongly sexually dimorphic; Lynch *et al.*, 1990), although we note the difficulty in differentiating between certain age and gender classes (such as small adult females and large male subadults). Work is currently underway to assess this aspect. It is likely, however, that the main application of infrared technology will be in monitoring otter activity.

Data generated from infrared counters in combination with spraint surveys could help in establishing whether a definitive relationship exists between otter activity and the abundance of otter field signs, an issue of continuing debate (Kruuk, 1995; Carss, Elston & Morley, 1998; Ruiz-Olmo *et al.*, 2001). Such information might facilitate the development of a predictive tool for estimating otter population size based solely on field-sign occurrence, similar to that currently applied to other endangered riparian mammals (e.g. water vole *Arvicola terrestris*; Woodroffe, Lawton & Davidson, 1990).

Activity indices derived from infrared counters deployed throughout river catchments could help to better assess and detect seasonal trends in demography or in activity patterns, perhaps in relation to changes in habitat quality or in riparian development. Such real-time data would be particularly useful to river managers involved in wildlife conservation, facilitating the protection of areas of greatest 'value' to otters and other riparian mammals. Likewise, the impact of riparian development on otter behaviour, activity and distribution could be assessed both pre- and post-development using a network of submerged counters.

Estimates of otter swimming speeds obtained from infrared counters will be potentially valuable in advising the design of instream structures. For example, it is thought that otters are sometimes forced to cross roads and risk being killed by passing vehicles because water velocities through bridges or culverts may be too high to allow for underwater passage (Strachan & Jefferies, 1996). By recording otter swimming speeds and incorporating flow meters into infrared counters, otter activity relative to water velocity could be assessed. This information could prove extremely useful when designing bridge and culvert systems to ensure that such structures do not restrict otter movements, thereby helping to reduce road kills at potentially dangerous 'hotspots'.

The techniques used in this study involved little or no encroachment into the otters' habitat and no disturbance to the study animals. Hence, data generated non-intrusively by infrared counters represent an improvement over other, more intrusive monitoring methods that relied on the trapping and tagging of individuals, or the periodic removal of scented spraints (Kruuk *et al*., 1986), used for resource signalling (Kruuk, 1992). Moreover, as data are gathered and stored remotely with little human supervision, image-capture systems provide a powerful and cost-effective alternative for monitoring otter activity in remote areas, where other techniques might be unsuitable or too costly (e.g. Cutler & Swann, 1999).

In summary, our study indicates that the use of submerged infrared counters represents a valuable, non-intrusive addition to the suite of techniques and methodologies currently used for monitoring elusive aquatic animals such as the Eurasian otter. It is likely that this technique may have similar utility for studying other endangered mustelids such as the hairy nosed otter *Lutra sumatrana*, the smooth-coated otter *Lutra perspicillata* or the European mink *M. vison*, although careful validation would be clearly required for each target species.

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References

Banks, S.C., Finlayson, G.R., Lawson, S.J., Lindenmayer, D.B., Paetkay, D., Ward, S.J. & Taylor, A.C. (2005). The effects of habitats fragmentation due to forestry plantation establishment on the demography and genetic variation of a marsupial carnivore *Antechinus agilis*. *Biol. Conserv*. **122**, 581–597.

Beja, P.R. (1996). Temporal and spatial patterns of rest-site use by four female otters *Lutra lutra* along the south-west coast of Portugal. *J. Zool. (Lond.)* **239**, 741–753.

Belant, J.L. (2003). A hairsnare for forest carnivores. *Wildl. Soc. Bull*. **31**, 482–485.

Carss, D.N., Elston, D.A. & Morley, H.S. (1998). The effects of otter (*Lutra lutra*) activity on spraint production and composition: implications for models which estimate prey-size distribution. *J. Zool. (Lond.)* **244**, 295–302.

Carss, D.N., Kruuk, H. & Conroy, J.W.H. (1990). Predation on adult Atlantic salmon, *Salmo salar* L., by otters, *Lutra lutra* (L.), within the River Dee system, Aberdeenshire, Scotland. *J. Fish Biol*. **37**, 935–944.

Chanin, P. (1985). *The natural history of otters*. London: Croom Helm.

Coakes, A., Gowans, S., Simardi, P., Giard, J., Vashro, C. & Sears, R. (2005). Photographic identification of fin whales (*Balaenoptera physalus*) off the Atlantic Coast of Nova Scotia, Canada. *Mar. Mamm. Sci*. **21**, 323–326.

Cutler, T.L. & Swann, D.E. (1999). Using remote photography in wildlife ecology: a review. *Wildl. Soc. Bull*. **27**, 571–581.

Dallas, J.F., Coxon, K.E., Sykes, T., Chanin, P.R.F., Marshall, F., Carss, D.N., Bacon, F.J., Piertney, F.B. & Racey, P.A. (2003). Similar estimates of population genetic composition and sex ratio derived from carcasses and faeces of Eurasian otter *Lutra lutra*. *Mol. Ecol*. **12**, 275–282.

Davison, A., Birks, J.D.S., Brookes, R.C., Braithwaite, T.C. & Messenger, J.E. (2002). On the origin of faeces: morphological versus molecular methods for surveying rare carnivores from their scats. *J. Zool. (Lond.)* **257**, 141–143.

Gill, R.M.A., Thomas, M.L. & Stocker, D. (1997). The use of portable thermal imaging for estimating deer population density in forest habitats. *J. Appl. Ecol*. **34**, 1273–1286.

González-Esteban, J., Villate, I. & Irizar, I. (2004). Assessing camera traps for surveying the European mink, *Mustela lutreola* (Linnaeus, 1761), distribution. *Eur. J. Wildl. Res*. **50**, 30–33.

Gorman, M.L., Kruuk, H., Jones, C., McLaren, G. & Conroy, J.W.H. (1998). The demography of European otters *Lutra lutra*. In *Behaviourand ecology of riparian mammals*: 107–118. Dunstone, N. & Gorman, M. (Eds). Cambridge: Cambridge University Press.

Green, J., Green, R. & Jefferies, D.J. (1984). A radio-tracking survey of otters *Lutra lutra* on a Perthshire river system. *Lutra* **27**, 85–145.

Heffner, R.A., Butler, M.J.IV & Reilly, C.K. (1996). Pseudoreplication revisited. *Ecology* **77**, 2558–2562.

Jenkins, D. & Harper, R.J. (1980). Ecology of otters in Northern Scotland. 2. Analyses of otter (*Lutra lutra*) and mink (*Mustela vison*) feces from Deeside, NE Scotland in 1977–78. *J. Anim. Ecol*. **49**, 737–754.

Jones, L.L.C. & Raphael, M.G. (1993). *Inexpensive camera systems for detecting martens, fishers, and other animals:*

guidelines for use and standardization. Oregon: United States Forest Service.

Karanth, K.U., Chundawat, R.S., Nichol, J.D. & Kumar, N.S. (2004). Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture–recapture sampling. *Anim. Conserv*. **7**, 285–290.

Karanth, K.U. & Nichols, J.D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* **79**, 2852–2862.

Karczmarski, L., Wursig, B., Gailey, G., Larson, K.W. & Vanderlip, C. (2005). Spinner dolphins in a remote Hawaiian atoll: social grouping and population structure. *Behav. Ecol*. **16**, 675–685.

Kruuk, H. (1992). Scent marking by otters (*Lutra lutra*): signaling the use of resources. *Behav. Ecol*. **3**, 133–140.

Kruuk, H. (1995). *Wild otters. Predation and populations*. Oxford: Oxford University Press.

Kruuk, H. & Carss, D.N. (1998). Costs and benefits of fishing by a semi-aquatic carnivore, the otter *Lutra lutra*. In *Aquatic predators and their prey*: 10–16. Greenstreet, S.P.R. & Tasker, M.L. (Eds). Oxford: Fishing News Books.

Kruuk, H., Carss, D.N., Conroy, J.W.H. & Gaywod, M.J. (1998). Habitat use and conservation of otters (*Lutra lutra*) in Britain. In *Behaviour and ecology of riparian mammals*: 119–134. Dunstone, N. & Gorman, M.L. (Eds). Cambridge: Cambridge University Press.

Kruuk, H., Conroy, J.W.H., Glimmerveen, U. & Ouwererk, E.J. (1986). The use of spraints to survey populations of otters *Lutra lutra*. *Biol. Conserv*. **35**, 187–194.

Kruuk, H., Gorman, M. & Parish, T. (1980). The use of 65-Zn for estimating populations of carnivores. *Oikos* **34**, 206–208.

Kruuk, H., Moorhouse, A., Conroy, J.W.H., Durbin, L. & Frears, S. (1989). An estimate of numbers and habitat preferences of otters *Lutra lutra* in Shetland, UK. *Biol. Conserv*. **49**, 241–254.

Lynch, J.M., Conroy, J.W.H., Kitchener, A.C., Jefferies, D.J. & Hayden, D.J. (1990). Variation in cranial form and sexual dimorphism among five European populations of the otter *Lutra lutra*. *J. Zool. (Lond.)* **238**, 81–96.

Macdonald, D. & Barrett, P. (1993). *Field guide to the mammals of Britain and Europe*. London: HarperCollins.

Mace, G.M., Baillie, J.E.M., Beissinger, S.R. & Redford, K.H. (2001). Assessment and management of species risk. In *Conservation biology. Research priorities for the next decade*: 11–29. Soulé, M.E. & Orians, G.H. (Eds). Washington: Island Press.

Mason, C.F. & Macdonald, S.M. (1986). *Otters: ecology and conservation*. Cambridge: Cambridge University Press.

Nolet, B.A., Wansink, D.E.H. & Kruuk, H. (1993). Diving of otters (*Lutra lutra*) in a marine habitat: use of depth by a single-prey loader. *J. Anim. Ecol*. **62**, 22–32.

Pfeiffer, P. & Culik, B.M. (1998). Energy metabolism of underwater swimming in river-otters (*Lutra lutra* L.). *J. Comp. Physiol. B: Biochem. Syst. Environ. Physiol*. **168**, 143–148.

Romanowski, J. & Brzezinski, M. (1997). How standard is the standard technique of the otter survey? *IUCN Otter Spec. Group Bull*. **14**, 57–61.

Ruiz-Olmo, J., Jiménez, J. & López-Martín, J.M. (1995). Radio-tracking of otters *Lutra lutra* in north-eastern Spain. *Lutra* **37**, 1–6.

Ruiz-Olmo, J., Saavedra, D. & Jiménez, J. (2001). Testing the surveys and visual track censuses of Eurasian otters (*Lutra lutra*). *J. Zool. (Lond.)* **253**, 359–369.

Shardlow, T.F. & Hyatt, K.D. (2004). Assessment of the counting accuracy of the Vaki infrared counter on chum salmon. *N. Am. J. Fish. Mgmt*. **24**, 249–252.

Sidorovich, V.E. (1991). Structure, reproductive status and dynamics of the otter population in Belorussia. *Acta Theriol*. **36**, 153–161.

Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffai, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gomez, H. & Ayala, G. (2004). The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx* **38**, 148–154.

Stearns, B.P. & Stearns, S.C. (1999). *Watching, from the edge of extinction*. London: Yale University Press.

Strachan, R. & Jefferies, D.J. (1996). *The otter survey of England 1991–1994*. London: Vincent Wildlife Trust.

Sutherland, W.J. (2002). Mammals. In *Ecological census techniques: a handbook*: 206–278. Sutherland, W.J. (Ed.). Cambridge: Cambridge University Press.

Terry, A.M.R. & McGregor, P.K. (2002). Census and monitoring based on individually identifiable vocalizations: the role of neural networks. *Anim. Conserv*. **5**, 103–111.

Wilson, G.J. & Delahay, R.J. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildl. Res*. **28**, 151–164.

Wires, L.R., Carss, D.N., Cuthbert, F.J. & Hatch, J.J. (2003). Transcontinental connections in relation to cormorant-fisheries conflicts: perceptions and realities of a "bête noire" (black beast) on both sides of the Atlantic. *Vogelwelt* **124**, 389–400.

Woodroffe, G.L., Lawton, J.H. & Davidson, W.L. (1990). Patterns in the production of latrines by the water vole (*Arvicola terrestris*) in the North Yorkshire Moors and their use as indices of abundance in population surveys. *J. Zool. (Lond.)* **220**, 439–445.