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Using first-passage time to link behaviour and habitat in foraging paths of a terrestrial predator, the racoon

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An understanding of how animals alter their behaviour in relation to environmental conditions is a key element in the study of animal movement, foraging ecology and habitat use, and can provide valuable information for practical conservation and management applications. To exploit resources in heterogeneous landscapes optimally, foragers should intensively search in profitable patches while minimizing foraging activities in low-quality areas. We used first-passage time (FPT) analysis to identify and characterize area-restricted search (ARS) behaviour along the nightly movement paths of racoons. While FPT analysis has been successfully applied to a variety of pelagic species, our goal was to determine the ability of FPT to detect habitat characteristics associated with changes in searching behaviour for a terrestrial predator. Racoons, *Procyon lotor*, were tracked via radiotelemetry during their nightly movements. We found evidence of ARS behaviour in 55 of 58 paths, with racoons concentrating intensive searching bouts in areas with an average radius of 42.6 m (range 20–100 m). To test whether our detection of ARS represented an actual change in behaviour, we tracked five racoons in relation to an artificial food patch. We detected ARS behaviour during 9 of 10 occasions in which a tracked animal encountered the food patch. Racoons showed ARS behaviour in areas with abundant shallow water, and they moved quickly through openings and dry areas with sparse ground-level vegetation. Application of this method should prove useful for studies of habitat use and foraging ecology of terrestrial predators by providing links between animal movements and the environment.

Animals live in spatially heterogeneous landscapes where resources are unevenly distributed across the environment in patches of varying scale within the context of the larger landscape (Johnson et al. 1992; Fauchald 1999). Predators should respond to this heterogeneity by spending more time in profitable patches with relatively high prey availability and spending less time searching for prey in less profitable areas (Stephens & Krebs 1986). One way that foragers may maximize time in profitable areas is by altering their search strategy as they move through the landscape. Specifically, an organism may move quickly and in a relatively linear fashion through nonprofitable areas, then adopt a more intensive searching strategy characterized by slower speeds and greater turning angles in response to stimuli, such as the location of a prey item. This behaviour is referred to as area-restricted search (ARS), and computer simulations have shown it to be an efficient method for locating and remaining in profitable areas when resources are not distributed homogenously in space (Benhamou 1992; Zollner & Lima 1999). Behaviour consistent with ARS has been observed in a variety of taxa, including insects (Kareiva & Odell 1987; Crist & MacMahon 1991), copepods (Leising & Franks 2002), birds (Smith 1974; Nolet & Mooij 2002; Paiva et al. 2010), spiders (Patt & Pfannenstiel 2009), fish (Mikio et al. 1994; Hill et al. 2000), as well as terrestrial and marine mammals (Lode 2000; Frair et al. 2005; Freitas et al. 2008), and may have evolved as an adaptive means of exploiting prey in heterogeneous environments (Scharf et al. 2009).

Studying the movements of individuals can provide insights into population-level characteristics (Kareiva & Odell 1987; Johnson et al. 1992; Turchin 1998; Mueller & Fagan 2008), and understanding search behaviour should be especially useful in working towards identifying links between behaviour and habitat. Because organisms should engage in intensive searching in areas that provide valuable resources, identifying the habitat characteristics associated with ARS should likewise identify habitat features important to a species in a given landscape, which could have important practical implications in wildlife management and conservation. Recent advances in animal-tracking technology have

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allowed ecologists to begin studying the relationships between movement behaviour and habitats of free-ranging vertebrates. Much of this work has focused on pelagic organisms such as turtles (McCarthy et al. 2010), marine mammals (Freitas et al. 2008) and seabirds (Pinaud & Weimerskirch 2005; Suryan et al. 2006; Weimerskirch et al. 2007; Hamer et al. 2009; Kappes et al. 2010; Paiva et al. 2010; Scheffer et al. 2010). Similar studies focusing on terrestrial vertebrates have been less common (Morales et al. 2004; Frair et al. 2005; Forester et al. 2007; Le Corre et al. 2008), with studies of terrestrial predators comparatively rare (Dickson et al. 2005; Valeix et al. 2010).

The racoon, *Procyon lotor*, is a primarily nocturnal generalist mesopredator whose behavioural and dietary plasticity allow it to exploit a wide variety of habitats. During late winter and spring, racoons in the southeastern portion of North America forage primarily on invertebrates, such as crayfish, before the soft mast of summer is available (Baker et al. 1945; Johnson 1970; Gehrt 2003). Invertebrate prey is not distributed evenly across the landscape; crayfish, for example, are a primarily aquatic organism and their availability to racoons is limited to areas with water that is shallow enough to allow racoons to access them. It could therefore be hypothesized that racoons should restrict their intensive searching to areas associated with abundant invertebrate prey, such as those offering shallow water and concentrations of crayfish. Here we use the method of first-passage time analysis (FPT) introduced by Fauchald & Tveraa (2003) to characterize ARS behaviour along the nightly movement paths of racoons, and subsequently link changes in movement behaviour to habitat features. The fine-scale movements of racoons have never been investigated in this manner, but observations describing long movements interrupted by periods of activity in confined areas suggest that racoons use ARS while foraging (Urban 1970; Hoffmann & Gottschang 1977; Greenwood 1982).

Our specific objectives were to determine whether racoons use ARS, describe the scale at which racoons engage in ARS, and discuss the viability of applying FPT analysis to detect the foraging movements of terrestrial predators. A number of methods to analyse how animal movements change in response to habitat have been developed in recent years, including state-space modelling (Jonsen et al. 2005), building mixtures of random walks (Morales et al. 2004), investigations of residence time (Barraquand & Benhamou 2008), impulse-response signal-filtering (Boettiger et al. 2011) and velocity-based movement modelling (Hanks et al. 2011). In comparison to many of these methods, FPT is relatively easy to implement and interpret. Secondly, we tested the hypothesis that ARS is linked to habitat by comparing the habitat characteristics of areas along movement paths in which racoons showed intensive searching to areas where racoons showed more extensive movements. If ARS is a response to prey resources whose availability is habitat specific, then habitat associated with intensive searching should differ from habitats in which racoons show rapid linear movements.

METHODS

Study Area

We conducted research on a 17 243 ha tract (hereafter Sherburne) of bottomland hardwood forest located in the Atchafalaya floodway system in south-central Louisiana, U.S.A. (30°30.2′N, 91°42.2′W). The study area was composed of 96% forest, 2% forest openings and 2% open water. Common overstory species included eastern cottonwood (*Populus deltoides*), nuttall oak (*Quercus texana*), water oak (*Quercus nigra*), overcup oak (*Quercus lyrata*), sweetgum (*Liquidambar styraciflua*), sugarberry (*Celtis laevigata*), green ash (*Fraxinus pennsylvanicus*), black willow (*Salix nigra*) and baldcypress (*Taxodium distichum*). Forest openings consisted of wildlife food plots, right-of-ways (electric and natural gas) maintained through mowing and herbicide application, levees and natural regeneration from forest harvesting. Because of levees and other water control structures Sherburne experienced no direct flooding from the Atchafalaya River; instead, river-induced flooding was manifested in the form of back-water flooding moving north from southern areas of the Atchafalaya Basin, and varied in severity from year to year. Most seasonal flooding on Sherburne could be attributed to local precipitation during the rainy season (February–April) as poorly drained alluvial soils allow surface water to persist for extended periods. Mean annual high and low temperatures for the region were 8.9 °C and 27.8 °C, respectively, and average annual rainfall was 155.4 cm.

Animal Capture and Movement Path Collection

We trapped racoons using wire-cage traps during 15 December 2007–10 March 2008 and 14 January 2009–21 February 2009 by placing traps in areas of suitable racoon habitat or in areas with signs of abundant racoon activity (i.e. tracks, scat). We trapped across the landscape in such a way as to ensure that radiotagged individuals occurred throughout the study area. We baited traps with various combinations of fish, corn and pastries, and we checked all traps daily within 4 h of sunrise. We anaesthetized racoons with ketamine hydrochloride at a rate of 10 mg/kg of estimated body mass (Bigler & Hoff 1974), and we recorded the gender of each individual and estimated age based on tooth wear (Grau et al. 1970) and overall body characteristics. We fitted all individuals at least 1 year old with a 50 g mortality-sensitive radiocollar (Advanced Telemetry Systems, Isanti, MN, U.S.A.) and released all racoons at their respective capture sites following processing and recovery. All capture and handling procedures were covered under Protocol Number AE2010-09 of the Institutional Animal Care and Use Committee of Louisiana State University.

We used sequential telemetry (hereafter focal runs) to obtain movement paths for individual racoons. A focal run consisted of recording a focal animal's location at 20 min intervals throughout the night (sunset to sunrise). We obtained locations by triangulation of azimuth readings taken from three to five spatial referenced locations using a hand-held three-element Yagi antenna and a receiver (Advanced Telemetry Systems). We used LOCATE III (Pacer; Truro, NS, Canada) to obtain Universal Transverse Mercator (UTM) coordinates for each triangulated location. We began all focal runs within 1 h of sunset and continued to track the focal animal until 1 h after sunrise, or until it reached its day-bed and ceased movements the following morning, which normally occurred within 1 h of sunrise. Our goal was to obtain a complete path representing the racoon's nightly movements. We terminated a focal run if the signal was lost on an animal, or if an observer's ability to confidently triangulate a location was otherwise compromised for at least 40 min (two sequential locations were missed). During eight focal runs, the focal racoon temporarily became inactive for short periods (1–3 h) in the middle of the night. In such cases we separated the nightly movements into two separate paths for analysis (from dusk until temporary den, and from temporary den until dawn). It was possible to distinguish active racoons from inactive racoons based on radio signal modulation; animals that were moving transmitted a wavering signal whereas inactive animals transmitted a steady signal (Greenwood 1982; M. E. Byrne & M. J. Chamberlain, personal observation). We feel confident of our ability to discern between resting and active animals based on our experiences during daytime den investigations, in which racoons that were inactive at a den would transmit