



Human disturbance affects personality development in a wild carnivore



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Human activity can dramatically affect personality traits in birds and small mammals. However, we know very little about how anthropogenic disturbance shapes personality in mammalian carnivores, and whether the personality traits that may be affected have fitness consequences in human-dominated landscapes. We adapted standard experiments commonly used to assess personality in captive animals to compare three personality traits in 72 wild juvenile spotted hyaenas, *Crocota crocuta*, living either in areas heavily disturbed by human activity or in areas with low levels of disturbance. We examined neophobia, defined as the tendency to avoid unfamiliar things, exploration, defined as the number of different ways an individual interacts with an object, and boldness, defined as an individual's tendency to take risks. To assess neophobia and exploration, we measured individuals' responses to a novel object, and to assess boldness, we measured the hyaenas' propensity to enter a wire-mesh box to obtain food. Juvenile spotted hyaenas living in low-disturbance areas were significantly more neophobic and less exploratory than individuals living in high-disturbance areas. This is consistent with results obtained with birds and small mammals; however, unlike these other taxa, hyaenas living in low-disturbance areas were bolder than individuals living in high-disturbance areas. The expression of some of these personality traits was also affected by the subject's social rank and the presence of a littermate, but not by subject age or sex. Of the three traits, only boldness predicted survival to adulthood: less bold individuals were significantly more likely to survive than bolder individuals, in both high-disturbance and low-disturbance habitats. We propose that behavioural or physiological maternal effects may be shaping offspring temperament differences related to disturbance.

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Human activity has been found to affect the behaviour of animals in a variety of ways. Some of the most pronounced effects have been documented on animals' personality or temperament traits, which are individual differences in behaviour that are stable across contexts and over time (Miranda, Schielzeth, Sonntag, & Partecke, 2013; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sol, Lapiedra, & González-Lagos, 2013). Changes in personality traits due to anthropogenic disturbance can result from individual behavioural plasticity or microevolutionary changes (Miranda et al., 2013). Across numerous bird and small mammal species, individuals tend to show more neophilic, exploratory, aggressive and bold personalities in urban areas than in rural areas (Miranda et al., 2013; Sol et al., 2013). However, we know virtually nothing about

whether or how human disturbance shapes personality in most other animals, including large mammalian carnivores.

There is a critical need to understand how human activity influences carnivore behaviour and populations (Baker, Boitani, Harris, Saunders, & White, 2008; Darrow & Shivik, 2009). Worldwide, carnivores are increasingly living in close proximity to humans (Bateman & Fleming, 2012; reviewed in Treves & Karanth, 2003; Treves, Wallace, Naughton-Treves, & Morales, 2006), resulting in more frequent predation on livestock, injury to humans and retaliatory killing of carnivores (Baker et al., 2008; Ripple et al., 2014). Understanding whether variation in personality affects carnivore survival in disturbed landscapes can help us to predict the effects of human activity on carnivore populations. Consistent interindividual differences in behaviour have been documented in a few wild adult carnivores (e.g. coyotes, *Canis latrans*: Harris & Knowlton, 2001; Heffernan, Andelt, & Shivak, 2007), but most studies have been conducted on captive individuals (maned wolves, *Chrysocyon brachyurus*: Silva & Azevedo, 2013; grey wolves,

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Canis lupus: Fox, 1972; MacDonald, 1983; Moretti, Hentrup, Kotschal, & Range, 2015; coyotes: Mettler & Shivik, 2007; European mink, *Mustela lutreola*: Haage, Bergvall, Maran, Kiik, & Angerbjörn, 2013; American mink, *Neovison vison*: Noer, Needham, Wiese, Balsby, & Dabelsteen, 2015; kowaris, *Dasyuroides byrnei*: Russell & Pearce, 1971; Wynne & McLean, 1999) or domestic animals (dogs, *Canis familiaris*: Draper, 1995; Jones & Gosling, 2005; cats, *Felis catus*: Durr & Smith, 1997). Understanding variation in personality among wild carnivores may also help researchers and managers to discern whether certain individuals consistently display behaviour patterns that put them at risk of conflict with humans, and to target such 'problem animals' for intervention (Caro, 1999; McDougall, Réale, Sol, & Reader, 2006; Shivik, 2006).

Few studies have assessed the fitness consequences of personality traits in areas disturbed by human activity (Archard & Braithwaite, 2010), although a number of recent studies have found that personality traits may be heritable and affect fitness in undisturbed habitats (Dall, Houston, & McNamara, 2004; Dingemanse, Both, Drent, & Van Oers, 2002; Kortet, Vainikka, Janhunen, Piironen, & Hyvärinen, 2014; Nicolaus et al., 2012; Petelle, Martin, & Blumstein, 2015; Smith & Blumstein, 2008; Taylor et al., 2012; Yoshida, Van Meter, & Holekamp, 2016). It has been hypothesized that, in disturbed areas, birds and small mammals with more neophilic, exploratory and bold personalities may have a fitness advantage, as these traits may allow them to exploit novel habitats, live at high population densities and take advantage of new resources (Miranda et al., 2013). However, the fitness consequences of these personality traits in areas with human activity may be dramatically different for carnivores than for birds or small mammals, as such tendencies would probably bring carnivores into direct conflict with humans.

Understanding whether personality traits in juvenile carnivores predict survivorship may be particularly important because young animals may be especially likely to engage in risky behaviour and end up in conflict with humans (Anderson, 1981; Saberwal, Gibbs, Chellam, & Johnsingh, 1994). Lack of hunting experience, tendency to prey on animals that are easy to kill and poor body condition relative to adults are all factors that might make juvenile carnivores prone to human–wildlife conflicts, such as depredation of livestock (Caro, 1994; Holekamp, Smale, Berg, & Cooper, 1997; Litvaitis, Clark, & Hunt, 1986; Matlack & Evans, 1992; Payne & Jameson, 1984; Seidensticker & McDougal, 1993; Stirling & Latour, 1978). Young dispersing males may be particularly prone to engage in such activities (Linnell, Odden, Smith, Aanes, & Swenson, 1999).

Here we used an experimental approach to explore variation in three personality traits in wild juvenile spotted hyaenas, *Crocuta crocuta*, and inquire whether these traits differ between hyaenas reared in habitat heavily disturbed by anthropogenic activity and those reared in areas with very low anthropogenic activity. Specifically, we examined neophobia, defined as the tendency to avoid or fear unfamiliar things (Barnett, 1958), exploration, defined as the number of different ways an individual interacts with an object (Glickman & Sroges, 1966), and boldness, defined as an individual's tendency to take risks (Réale et al., 2007). We predicted that, if juvenile hyaenas living in areas with high human disturbance behaved like 'urbanized' birds and small mammals (Miranda et al., 2013; Sol et al., 2013), they would be less neophobic, more exploratory and bolder than juveniles in low-disturbance areas. In addition to human disturbance, we explored the effects of sex and social rank on juvenile personality traits because these variables begin to shape hyaena behaviour early in life (Dloniak, French, & Holekamp, 2006; Holekamp, Swanson, & Van Meter, 2013; Smale, Holekamp, Weldele, Frank, & Glickman, 1995). We also explored the effects of age on expression of these personality traits because,

even though all of our subjects were juveniles, neophobia, exploration and boldness change in some species as individuals approach reproductive maturity (Biondi, Bó, & Vassallo, 2010; Kendal, Coe, & Laland, 2005). Finally, we tested for consistency in behaviour across time and context, and inquired whether any of these personality traits predicted survival to reproductive maturity.

METHODS

Subjects and Study Populations

Study subjects were 72 juvenile spotted hyaenas inhabiting two protected areas in the Mara-Serengeti ecosystem in southwestern Kenya. Fifty-eight of these juveniles were subjects in our tests of neophobia and exploration and 60 of them were subjects in our test of boldness; 45 participated in both tests. Roughly half of the subjects (59% for tests of neophobia and exploration, 50% for test of boldness) lived in three clans whose territories were located in The Mara Conservancy, a pristine area managed by a private nonprofit organization that strictly prohibits cattle grazing and human presence except in tour vehicles. We will therefore refer to this area as 'low disturbance'. The remaining subjects were from a clan that has been continuously monitored since 1988, and lives just inside the border of the Masai Mara National Reserve. We refer to this area as 'high disturbance' because, since the late 1990s, there has been exponential human population growth along the border of the reserve (Watts & Holekamp, 2009), humans are active with their livestock both day and night inside the reserve in this area and direct conflict between hyaenas and livestock is common both inside and outside the reserve (Kolowski & Holekamp, 2006). Since 2005, humans have been responsible for the majority of hyaena deaths (through spearing, snaring and poisoning) for which mortality sources can be determined (Holekamp & Dloniak, 2010). Through historical analyses and comparative studies with populations living in more pristine areas, numerous behavioural effects of increased human activity have been documented in this population, including increased nocturnality, increased daily travel, lower rates of den attendance by mothers, active avoidance of livestock and herders, and a preference for areas with dense vegetative cover (Boydston, Kapheim, Watts, Szykman, & Holekamp, 2003; Kolowski & Holekamp, 2009; Kolowski, Katan, Theis, & Holekamp, 2007.).

Our subjects ranged in age from 50 to 463 days old (mean = 171 days, median = 153 days). Spotted hyaenas do not reach reproductive maturity until after ~720 days of age, nor do they reach full morphological maturity before 1000 days of age. All subjects could be individually identified based on unique spot patterns and ear damage. Age was initially estimated when cubs were first observed, based on their appearance and size (Holekamp, Smale, & Szykman, 1996), and sex was determined based on the shape of the glans of the erect phallus (Frank, Glickman, & Powch, 1990). However, two subjects died before we could determine their sex and were excluded from our models.

Each juvenile was assigned a social rank based on our observations of its mother's position in the clan's dominance hierarchy. Observations of each adult female's aggressive and submissive behaviours during dyadic agonistic interactions were used to construct the hierarchy, as described previously (Martin & Bateson, 1988; Smale, Frank, & Holekamp, 1993). Juveniles 'inherit' dominance ranks immediately below those of their mothers in a process of social learning that is not complete until at least 18 months of age (Holekamp & Smale, 1993; Smale et al., 1993). Hyaenas of both sexes retain their maternal ranks as long as they reside in the natal clan, which females do throughout their lives, but most males

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