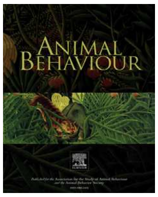
Animal Behaviour 132 (2017) 303–312

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Human disturbance affects personality development in a wild carnivore

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ARTICLE INFO

Article history:
Received 25 January 2017
Initial acceptance 20 February 2017
Final acceptance 30 June 2017
Available online 26 September 2017
MS. number: A17–00088R

Keywords:
anthropogenic disturbance
Crocuta crocuta
human–wildlife conflict
neophobia
personality
social rank
spotted hyaena
temperament

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, *Crocuta 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.

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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http://dx.doi.org/10.1016/j.anbehav.2017.08.023
0003-3472/

Canis lupus: Fox, 1972; MacDonald, 1983; Moretti, Hentrup, Kotrschal, & 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 disperse to new clans at 2–5 years of age (Frank, 1986; Holekamp & Smale, 1998).

We conducted our tests on groups of individuals at communal dens, where juvenile hyaenas live together and are rarely found alone. Spotted hyaenas give birth to litters containing one or two cubs at isolated natal dens. However, when cubs are 3–4 weeks of age, mothers move them to a communal den, where they live for the next 7–12 months. The communal den is a complex of underground tunnels and chambers that cannot be entered by adults. However, juveniles emerge from the warmth and safety of the den daily to nurse from their mothers and socialize near the den with clanmates (Holekamp & Dloniak, 2010; Holekamp & Smale, 1998). Mothers select protective den sites (Boydston, Kapheim, & Holekamp, 2006) such that hyaenas in neither high- nor low-disturbance areas experience direct exposure to humans or anthropogenic activity at their dens aside from occasional visits by tour vehicles, to which subjects in both high- and low-disturbance areas are well habituated.

Experimental Stimuli

We used a novel object test to measure neophobia and exploration, and a baited box test to measure boldness. In the novel object test, we used one of four objects (Fig. 1). Each object was approximately 0.3 m tall when deployed. Novel objects were chosen that juveniles would be highly unlikely to encounter otherwise, even if they had begun to spend time away from the communal den and even if they lived in areas with human activity. Because test sessions often involved multiple individuals, we varied the object being used to ensure that it was novel to the individuals being tested.

In the baited box test, we used a metal mesh box (70 × 40 cm and 44 cm high) with one open side large enough for cubs to enter (Fig. 2). The box had no bottom surface except for a metal tray (20 × 40 cm) at the back end of the box where we could sprinkle a layer of powdered milk (15 ml), which young hyaenas prefer over other food rewards. Cubs could only reach the powdered milk to feed if they fully entered the box. Prior to baited box test sessions, we familiarized individuals with powdered milk by liberally distributing it around each active communal den on three separate occasions when no hyaenas were present above ground. Although we did not systematically observe and record whether each subject consumed powdered milk prior to testing, we assumed that any juveniles actively using the den would be exposed to the scent and taste of milk on at least one of these three occasions.

Ethical Note

All subjects were free living, and were thus free to choose whether or not to interact with the stimuli we presented. The study was conducted in compliance with Kenyan law and guidelines for work with mammals provided by the American Society of Mammalogists (Sikes et al., 2016). The work was conducted under IACUC approval number 05/14–087–00 from Michigan State University and Research Clearance number NACOSTI/P/14/ 2154/1323 from the Kenyan Commission on Science, Technology and Innovation.

Figure 1. The four objects used for the novel object test to measure neophobia and exploration. Each object was approximately 0.3 m tall when deployed. The cooler, the funnel and the stool were plastic, and the bucket was metal. Novel objects were chosen that juveniles would be highly unlikely to encounter otherwise.

Figure 2. The metal box used for the baited box test to measure boldness (70 × 40 cm and 44 cm high). The box had no bottom surface except for a metal tray (20 × 40 cm) at the back end of the box where we could sprinkle a layer of powdered milk (15 ml). The box was open on one side, allowing a subject to walk in and fully enter the box in order to access the powdered milk at the back.

Data Collection

Experiments were conducted opportunistically during our two daily observation periods, in the morning (0600–1000 hours) and evening (1700–2000 hours). Stimuli were deployed from our research vehicles, to which all subjects were well habituated. In both the novel object test and the baited box test, we placed the stimulus approximately 20 m away from the den entrance. The stimulus was deployed either when no individuals were present above ground, or by positioning the research vehicle to block the view of any individuals present above ground. In the baited box test, the open side of the box was oriented towards the den entrance. All trials were videotaped from approximately 20 m away from the stimulus, using a Sony HDD Handycam Super Steady Shot HDR-SR11 mounted on a tripod affixed to our research vehicle. Trials were terminated when no new individuals entered within a 10 m radius of the stimulus for 5 min, or due to other logistical constraints (e.g. darkness or to prevent an individual from destroying an object).

Data Extraction

Behaviours were coded from the video footage using JWatcher 1.0 (Blumstein & Daniel, 2007). In each test session, any individual approaching within 10 m of the stimulus was considered a subject, and we coded each subject's behaviour for the entire time it was within 10 m of the stimulus. This cutoff distance allowed us to obtain high-quality footage of subjects' interactions with the stimuli.

In the novel object test, we operationally defined neophobia as the number of minutes it took a subject to contact the object after it had come within 5 m of the object (i.e. latency), as has been done in previous work assessing spotted hyaenas' approaches to novel stimuli (Benson-Amram & Holekamp, 2012). If a subject never contacted the object, its latency was calculated as the total time the subject was within 5 m of the object during the trial.

In the novel object test, we defined exploration as a subject's tendency to interact with the novel object in multiple different ways. We assigned each subject an ‘exploration score’, ranging from

0 to 4, based on how many exploratory behaviours it exhibited. Subjects received a score of 0 if they came within 10 m of the object but never contacted it. Subjects received a score of 1 if they contacted the object with their snout. Subjects received a score of 2 if they bit or licked the object in addition to contacting it with their snout. Subjects received a score of 3 if they displayed these two behaviours and, in addition, either pawed the object or picked it up. The majority of the subjects who received a score of 3 (seven of nine subjects) picked up the object but did not use their paws; nevertheless, we gave both behavioural combinations a score of 3. Subjects with a score of 4 displayed all four of these behaviours.

In the baited box test, we defined boldness as a subject's willingness to enter the box to feed on milk. We assigned subjects a ‘boldness score’, ranging from 0 to 3. Subjects received a score of 0 if they came within 10 m of the box but never contacted or entered it. Subjects received a score of 1 if they contacted the box but did not go inside. Subjects received a score of 2 if they entered the box partially, or entered the box fully but never attempted to feed. Subjects received a score of 3 if they entered the box completely and fed on the milk.

Statistical Analysis

Independent variables

We first ran a Cox proportional hazard model to inquire whether there were differences between the three clans in the low-disturbance area with respect to neophobia, and Kruskal–Wallis rank sum tests to determine whether there were any significant differences in either boldness or exploration between the three clans in the low-disturbance area. We then inquired whether neophobia, exploration and boldness were predicted by whether the subject lived in a high- or low-disturbance area, as well as by its age, sex and maternal rank. Age in days was included as a continuous variable. We assigned each subject the current social rank of its mother within the clan's dominance hierarchy on the day of testing. Ranks were standardized from −1 to 1, with the most dominant individual having a standardized rank of 1. None of our results changed if we calculated a subject's social rank relative only to the other individuals present in its specific test session. We also included time of day at testing (morning or evening) as a predictor variable.

We conducted the novel object and baited box tests on groups of individuals because juvenile hyaenas are almost never found alone at the communal den, and therefore we examined effects of several variables related to the social context of the testing situation. First, in our models for neophobia, exploration and boldness, we included as a variable the total number of subjects present in order to determine whether the presence of other hyaenas facilitated or interfered with an individual's interaction with the stimulus. In a small percentage of test sessions (4 of 18 novel object sessions and 2 of 17 box test sessions), in addition to test subjects, an adult was present and within 10 m of the stimulus at some point during the session. Although we did not analyse the behaviour of these individuals as subjects, we included them when assessing the social context of the test session by increasing the number of subjects present to account for them. Second, we included as a binary variable whether or not the subject had a littermate who was also a subject during the test because, in other species, littermates may be less fearful or inhibited when together than when apart (Bergmüller & Taborsky, 2010; Hudson, Bautista, Reyes-Meza, Montor, & Rödel, 2011; Stöwe, Bugnyar, Loretto, & Schloegl, 2006).

In our models for neophobia and boldness, we additionally included whether or not the subject had seen another individual contact the novel object or baited box before doing so itself or, if the subject did not contact the stimulus, whether it observed another subject contact the stimulus earlier during that test session. We did not include this as a variable in our model for exploration because we assumed that seeing another individual contact the novel object would be more likely to influence whether or not the subject contacted the object than to affect the diversity of behaviours performed during interactions with the object, which was our dependent variable. Furthermore, because our measures of neophobia and exploration were assessed from the same novel object test, we chose to examine the effect of seeing another individual contact the novel object in our analysis of neophobia, where the main behaviour of interest was a subject's willingness to approach and contact the object. However, our results did not change if we included this variable in our model for exploration.

Models of variation in neophobia, exploration and boldness

In statistical analysis of neophobia, we modelled variation in latency to contact the novel object using a Cox proportional hazards model in the ‘survival’ package in R (R version 3.3.1; Development Core Team, 2015). Our full model included the following predictor variables: age (in days), disturbance (high or low), social rank, sex, time of day (morning or evening), number of subjects present in the session, presence of a littermate and whether the subject observed another individual contact the object. A Cox proportional hazards model, originally developed for survival analyses, provides a method to analyse right-censored ‘time to event’ data. This approach allowed us to analyse the responses of those subjects that never touched the object together with those that did, instead of performing two separate analyses or assigning ‘time out scores’ to subjects that never contacted the object (Budaev, 1997; Jahn-Eimermacher, Lasarzik, & Raber, 2011). Right-censored latencies for the subjects that never contacted the novel object were specified in the model. This model assumes no underlying distribution of the latency measure, but it does assume that effects of predictor variables on the latency to respond are constant and additive. These assumptions were satisfied in our data set.

In statistical analysis of exploration and boldness, we treated subjects' scores as ordered categorical variables and used the ‘ordinal’ package in R to perform cumulative link models. These models, also known as proportional odds models or ordered regression models, assume intrinsic ordering in the levels of the response measure (in our case, from least bold or exploratory, to most bold or exploratory). Our full model for exploration included the following predictor variables: age (in days), disturbance (high or low), social rank, sex, time of day (morning or evening), number of subjects in the session and presence of a littermate. Our model for boldness included these same predictor variables plus the binary variable of whether or not the subject observed another individual contact the box. In both models, we also included each subject's total trial time as a covariate to control for variation between subjects in trial duration. We calculated the odds ratio for each predictor variable from the output of the models. Preliminary analyses indicated no effect of the object type (Fig. 1) on neophobia or exploration, so we did not include it as a factor in our analyses. All analyses were conducted in R (R version 3.3.1; Development Core Team, 2015). Parameter estimates were considered significant when $P \leq 0.051$.

Consistency across time and context

Due to the opportunistic nature of conducting these experiments, a subset of individuals participated twice in either the novel object test ($N = 14$) or the baited box test ($N = 14$). To examine individual consistency over time in neophobia, we looked exclusively at individuals who had participated in two novel object tests, each with a different object ($N = 14$). We did not analyse data for subjects who participated in two novel object tests with the same object, as the stimulus was no longer novel to the subject in its second test. Because we had data points that were right-censored when an individual never contacted the object, we used an extension of the Cox proportional hazards model from our analysis of initial trials, described above. We incorporated a random effect of subject identity into a Cox proportional hazards model using a shared gamma frailty model (Wienke, 2011). We also included exposure number (first or second) as a fixed effect, and any variables that had significant parameter estimates in our analysis of first trial responses. We then used Akaike's Information Criterion corrected for small sample sizes (AICc) to compare the fit of this frailty model to the fit of a Cox proportional hazards model that did not include subject identity. A smaller AICc value indicated a better fit. We also calculated a parameter estimate for the effect of subject identity using a likelihood ratio test.

To examine individual consistency over time in exploration and boldness, we again analysed responses for only the 14 subjects that participated twice in a test. We used a repeated measures ANOVA, with the subject's exploration or boldness score as the response measure. We included as a predictor variable whether the trial was a subject's first or second exposure, as well as the predictor variables that had significant parameter estimates in our analysis of first trial responses. To estimate repeatability, defined as the proportion of total variance accounted for by the subject's identity (Lessells & Boag, 1987), we calculated intraclass correlation coefficients (ICC), and associated confidence intervals according to Wolak, Fairbairn, and Paulsen (2011) using the ‘ICC’ package in R.

We examined consistency in neophobia across contexts for subjects who were tested in both a novel object test and a box test ($N = 45$). To do this, we treated the box as a fifth novel stimulus and inquired whether there was a significant correlation between a subject's latency to approach a novel object and its latency to approach the box baited with food. We calculated each subject's latency to contact or enter the box, whichever came first, after coming within 5 m of it. We then fit a shared gamma frailty model, similar to the one described above, modelling subject as a random effect, and including as fixed effects the type of test (novel object or box), exposure number (first or second) and variables that had significant parameter estimates in our analysis of neophobia in first trial responses. Using AICc, we compared this model to a model that did not incorporate subject identity, and calculated a parameter estimate for subject identity using a likelihood ratio test.

Relationship between personality traits and survival

Using our demographic records, we determined whether each subject survived to reproductive maturity (2 years of age); all subjects could potentially have reached this age by the time this analysis was conducted. We then used three different generalized linear models (GLM) to determine whether performance in each of the temperament tests predicted the log odds of a subject surviving to reproductive maturity. We used the ‘GLM’ package in R and specified a binomial distribution. In our model for neophobia, latencies to contact the novel object were included as a predictor variable and were right-censored for subjects that never contacted the object. In our analyses testing whether exploration or boldness predicted survival to maturity, exploration scores or boldness scores were included as predictor variables in the GLM model. In each of the three models, we also included maternal rank, sex and level of disturbance (high or low) as predictor variables. We also included the age at testing as a covariate in each model, but it did not significantly correlate with survival, so we report the results of our models without controlling for age at testing. To further test whether the relationship between each of the three personality traits and survival was mediated by the degree of human disturbance, or the subject's sex, or social rank, we used AICc to compare the fit of our full models to models including interaction terms between each of these factors and the score on the personality test (latency to contact the object for neophobia, exploration score or boldness score).

RESULTS

Preliminary analysis indicated that subjects did not differ between the three clans in the low-disturbance area in their neophobia (Wald test: $H_3 = 2.68$, $P = 0.44$), exploration ($H_2 = 4.75$, $P = 0.09$), or boldness ($H_2 = 3.77$, $P = 0.15$). In subsequent analysis, we therefore treated all individuals from clans in low-disturbance areas together as we compared them to juveniles in the clan living in the high-disturbance area.

Neophobia

Fifty-eight juveniles participated in the novel object test across 18 test sessions, and 69% (40 of 58) of these individuals contacted the object. The Cox proportional hazards model was significant (Wald test: $H_8 = 26.2$, $N = 58$, $P < 0.001$), indicating that subjects in the high-disturbance area were significantly less neophobic than subjects in low-disturbance areas (Table 1, Fig. 3a). The model also indicated that high-ranking juveniles were less neophobic than low-ranking juveniles ($P = 0.002$; Fig. 3b), and that juveniles with a littermate present were less neophobic than other juveniles ($P = 0.032$). Subjects were also less neophobic in evening than in morning sessions ($P = 0.011$), and in sessions where more hyaenas were present ($P = 0.043$). Surprisingly, subjects were significantly more neophobic if they saw another individual contact the object earlier in the session ($P = 0.036$).

Exploration

Exploration scores in the novel object test varied from 0 to 4 ($N = 58$). Eighteen subjects received a score of 0 (31%), 13 subjects received a score of 1 (22%), seven subjects received a score of 2 (12%), nine subjects received a score of 3 (16%) and 11 subjects received a score of 4 (19%; Fig. 4). The logistic regression model indicated significant effects of disturbance and rank on exploration behaviour (Table 2). Specifically, individuals in the high-disturbance area were significantly more exploratory than individuals in the low disturbance area (Fig. 4a), and high-ranking individuals were more exploratory than low-ranking individuals (Fig. 4b). There was a significant positive association between exploration and trial duration, and subjects were significantly more exploratory in the evenings than in the mornings.

Table 1
Results of a Cox proportional hazards model for variation in latency to contact the novel object ($N = 58$)

	Hazard ratio (exp(β))	Coefficient	SE	z	P
Age	1.00	0.0002	0.002	0.12	0.936
Disturbance	1.96	0.67	0.35	1.95	0.051*
Social rank	2.78	1.02	0.33	3.07	0.002*
Sex	1.21	0.19	0.36	0.54	0.597
Time of day	2.96	1.08	0.43	2.53	0.011*
No. of subjects in session	1.16	0.15	0.08	2.02	0.043*
Littermate present	2.36	0.86	0.40	2.15	0.032*
Observe another subject make contact	0.39	−0.95	0.45	−2.10	0.036*

*$P \leq 0.051$.

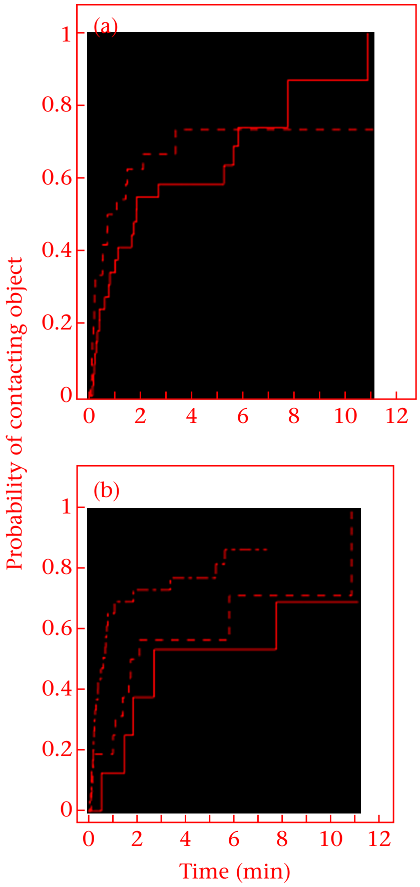

Figure 3. Cox proportional hazards models examining juvenile hyaenas' (a) probability of contacting the novel object in high-disturbance areas (dashed line) and low-disturbance areas (solid line; $P = 0.05$) and (b) latency to contact the object based on social rank ($P = 0.002$). Social rank was analysed statistically as a continuous variable but is shown here by dividing the clan's hierarchy into three dominance classes: the high-rank category includes ranks 1.00 to 0.33 (dash-dot line), the middle-rank category includes ranks 0.33 to −0.33 (dashed line) and the low-rank category includes ranks −0.33 to −1.00 (solid line).

Boldness

Sixty juveniles participated in the boldness box test, and boldness scores varied from 0 to 3. Nineteen subjects received a score of 0 (31%), 10 subjects received a score of 1 (17%), 10 subjects received a score of 2 (17%) and 21 subjects received a score of 3 (35%). The logistic regression model indicated that subjects in low-disturbance areas were significantly bolder than individuals in high-disturbance areas (Table 3, Fig. 5). There was a significant positive association between boldness and trial duration ($P = 0.0006$), and a trend for females to be bolder than males ($P = 0.066$), but we observed no effects of rank on boldness.

Consistency Across Time and Context

For neophobia, our frailty model containing the random effect of subject identity was a significantly better fit than the model without subject identity as a factor, indicating significant repeatability in subjects' neophobia across trials ($\chi^2_1 = 10.99$, $P = 0.006$). Subjects' latency to contact a novel object did not change significantly across exposures (hazard ratio = 0.94, $P = 0.92$). For exploration, the repeated measures ANOVA similarly indicated that subjects' exploratory behaviour did not change significantly across exposures, as indicated by a nonsignificant within-subjects

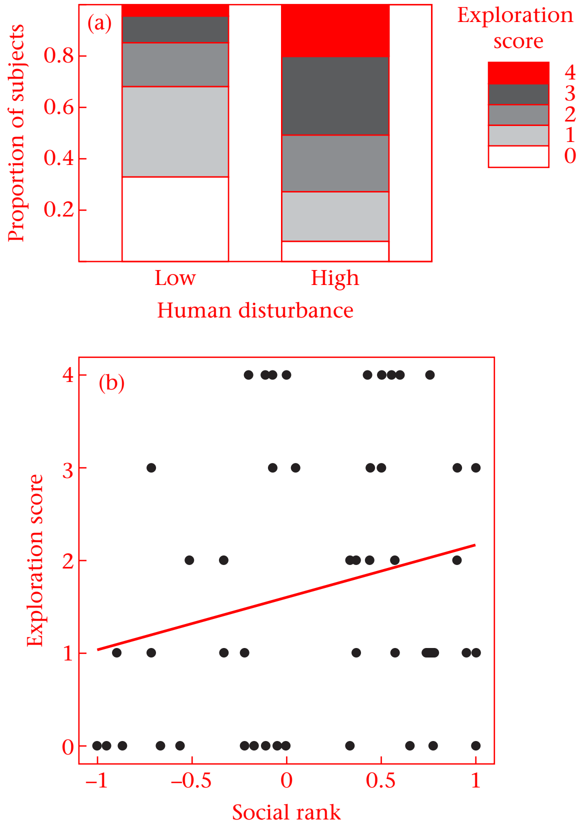

Figure 4. Logistic regression models examining variation in juvenile hyaenas' exploration scores (a) between high- and low-disturbance areas ($P = 0.003$) and (b) between high- and low-ranking individuals ($P = 0.020$; $N = 58$).

Table 2
Results of a logistic regression model for variation in exploration of the novel object ($N = 58$)

	Odds ratio	Coefficient	SE	*z*	*P*
Trial duration	1.22	0.20	0.06	3.49	0.0005*
Age	1.00	0.001	0.003	0.36	0.718
Disturbance	6.37	1.85	0.63	2.95	0.003*
Social rank	2.93	1.08	0.46	2.32	0.020*
Sex	1.87	0.62	0.58	1.08	0.282
Time of day	5.62	1.72	0.63	2.73	0.006*
No. of subjects in session	1.21	0.19	0.13	1.52	0.129
Littermate present	1.70	0.53	0.60	0.89	0.375

$^*P \le 0.051$.

Table 3
Results of a logistic regression model for variation in boldness ($N = 60$)

	Odds ratio	Coefficient	SE	*z*	*P*
Trial duration	1.15	0.15	0.04	3.44	0.0006*
Age	0.99	−0.01	0.005	−1.40	0.161
Disturbance	0.22	−1.50	0.64	−2.34	0.019*
Social rank	0.74	−0.30	0.46	−0.77	0.440
Sex	0.28	−1.31	0.71	−1.84	0.066
Time of day	1.05	−0.02	0.88	−0.03	0.980
No. of subjects in session	0.97	−0.01	0.12	−0.12	0.910
Littermate present	1.35	0.36	0.57	0.63	0.529
Observe another subject enter or contact box	2.45	0.79	0.87	0.91	0.365

$^*P \le 0.051$.

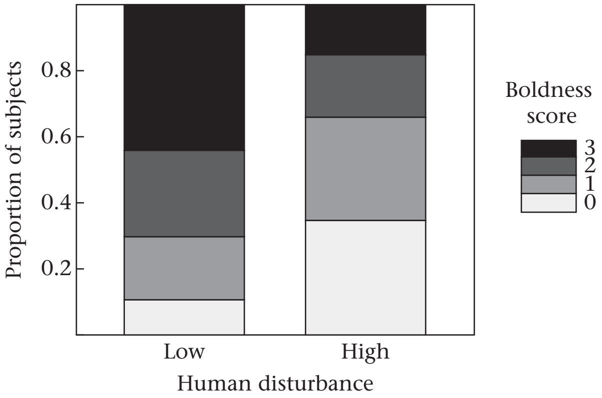

Figure 5. Logistic regression model examining variation in boldness scores for juveniles in high- and low-disturbance areas ($P = 0.019$; $N = 60$).

parameter estimate for exposure number ($F_{1,11} = 0.258$, $P = 0.62$). However, the repeatability estimate for exploration was also nonsignificant ($r = 0.20$, CI $= -0.34$, 0.64). For boldness, the repeated measures ANOVA indicated that subjects' boldness did not change significantly across repeated trials, as indicated by a nonsignificant within-subjects parameter estimate for exposure number ($F_{1,12} = 0.222$, $P = 0.424$). The repeatability estimate for boldness was significant ($r = 0.78$, CI $= 0.45$, 0.92). Thus, juvenile spotted hyaenas appear to show consistency over time in their neophobia and boldness, but not in their degree of exploration.

In our assessment of consistency in neophobia in two different contexts, namely a subject's latency to contact the novel object and latency to contact or enter the baited box, our frailty model with subject identity as a random effect was a significantly better fit than our model without subject identity as a factor ($\chi^2_1 = 28.1$, $P = 0.002$). This indicates significant individual consistency in subjects' neophobia when encountering novel stimuli that offer a food reward and those that do not. Subjects had significantly shorter latencies to approach the stimulus on the second test they received than on their first test (hazard ratio $= 2.33$, $P = 0.001$) regardless of whether it was the novel object test or baited box test (hazard ratio $= 1.20$, $P = 0.513$).

Relationship Between Personality Traits and Survival

Of the 58 subjects in the novel object test, 39 (67%) survived to reproductive maturity. Latency to contact the object ($\beta = 1.20$, $P = 0.22$) did not predict survival to maturity, but juveniles in low-disturbance areas were more likely to survive than juveniles in high-disturbance areas ($\beta = 0.18$, $P = 0.018$), and juveniles of high rank were more likely to survive than juveniles of low rank ($\beta = 4.59$, $P = 0.02$). Sex did not predict survival ($\beta = 0.61$, $P = 0.49$). Exploration score also failed to predict survival to reproductive maturity ($\beta = 0.91$, $P = 0.70$), but again subjects in low-disturbance areas were significantly more likely to survive than subjects in high-disturbance areas ($\beta = 0.18$, $P = 0.02$), and survival was significantly positively correlated with social rank ($\beta = 4.34$, $P = 0.015$). Sex did not predict survival to reproductive maturity ($\beta = 0.65$, $P = 0.54$). Models that included interactions between the temperament traits and the other predictor variables did not fit the data significantly better than our model without interactions.

Of the 60 subjects tested in the baited box test, 40 (67%) survived to reproductive maturity. Boldness affected survival similarly in both disturbed and undisturbed areas. Subjects who were less bold were significantly more likely to survive ($\beta = 0.49$, $P = 0.05$), and a model that included boldness was a significantly better fit than one that did not (likelihood ratio test: $\chi^2_1 = -4.51$, $P = 0.034$). In this sample, individuals in low-disturbance areas were again significantly more likely to survive than individuals in high-disturbance areas ($\beta = 0.075$, $P = 0.004$). Higher-ranking individuals were also more likely to survive than lower-ranking individuals ($\beta = 3.91$, $P = 0.03$), but sex did not predict survival to reproductive maturity ($\beta = 0.47$, $P = 0.36$). Models that included interactions between boldness and the other predictor variables failed to fit the data significantly better than our model without interactions.

DISCUSSION

Our findings are consistent with the growing literature demonstrating the profound influence that human disturbance can have on personality traits in wild populations, and permit comparisons with other taxa that have been more thoroughly studied. We found significant effects of human disturbance on all three of the juvenile personality traits we measured in spotted hyaenas. Patterns in neophobia and exploration were similar to those documented in comparisons of urban and rural individuals among birds and small mammals (Miranda et al., 2013; Smith & Blumstein, 2008; Sol et al., 2013): juvenile hyaenas in low-disturbance areas were significantly more neophobic and less exploratory than juveniles in high-disturbance areas. However, in contrast to these other taxa, juvenile spotted hyaenas in low-disturbance areas were significantly bolder than those in high-disturbance areas.

Our results also demonstrate that personality traits, although often challenging to measure in lone individuals in the field, can be effectively assessed in a group context. Conducting personality tests in group contexts rather than in isolation enhances ecological validity for individuals who are always in a social group (Drea, 2006), and better indicates how personality traits are actually expressed in free-living animals than testing subjects alone (Webster & Ward, 2010). We were able to account for the effects of social context by measuring situational variables and including them in our statistical models. Neophobia and boldness, but not exploration, showed significant repeatability within the juvenile period. We also found evidence for consistency in neophobia across contexts. Among juveniles that participated in both the novel object and baited box tests, latencies to contact the stimuli were highly consistent.

In addition to human disturbance, maternal rank emerged as an important factor shaping juvenile personality traits in spotted hyaenas. The relationship between social rank and personality varies among species, and our finding that higher-ranking juveniles were less neophobic and more exploratory than low-ranking juveniles is consistent with some previous studies (David, Auclair, & Cézilly, 2011; Mettler & Shivik, 2007), but not others (An, Kriengwatana, Newman, MacDougall-Shackleton, & MacDougall-Shackleton, 2011; Fox, Ladage, Roth, & Pravosudov, 2009; Gómez-Laplaza, 2002). That there was still a significant effect of rank when we calculated subjects' ranks relative only to those of the other subjects present in a specific test session suggests that the influence of rank was not dependent on the immediate social context of the test; low-ranking individuals were more neophobic and less exploratory even when they happened to be among the highest-ranking subjects present in a particular test session. Maternal rank, therefore, appears to shape personality traits from a young age, as it does offspring growth, aggression and play (Dloniak et al., 2006; Hofer & East, 2003; Holekamp et al., 2013; Lewin, Swanson, Williams, & Holekamp, 2016).

It is perhaps surprising that we found no relationship between maternal rank and boldness, as high-ranking individuals could potentially have dominated access to the powdered milk in the baited box test by attacking lower-ranking subjects. Yoshida et al. (2016) found that rank and boldness, as measured by individuals' closest approach to lions, *Panthera leo*, during lion–hyaena interactions, were significantly positively related in females but not in males. Our results might be due to the fact that juveniles are still in the process of learning which conspecifics they can appropriately dominate or displace from food. Additionally, although a low-ranking juvenile subject may have had to wait for a higher-ranking subject to enter the box and feed first, when the higher-ranking animal left the box, the scent of milk probably still attracted lower-ranking subjects, which could still scrounge for remaining milk and thus receive the highest boldness score. It seems unlikely that juveniles in low-disturbance areas are bolder than those in high-disturbance areas because they are hungrier, as has been found in other studies (Biro & Booth, 2009; Chapman, Morrell, & Krause, 2010). If hunger were primarily driving the expression of boldness in our test, we would expect lower-ranking individuals to be bolder than higher-ranking individuals, who are generally better fed. We would also expect individuals to be less bold in trials conducted in the morning than in the evening, when juveniles typically have not nursed since the morning, so they should be more highly motivated to reach the milk in our test apparatus. However, neither time of day nor rank significantly predicted boldness.

Neophobia was the only trait significantly affected by the presence and behaviour of conspecifics. Subjects were less neophobic when more subjects were present in the test session, which is consistent with the behaviour of hyaenas solving a puzzle box problem (Benson-Amram & Holekamp, 2012), the important role of social facilitation in hyaena social behaviour (Glickman et al., 1997) and results of novel object tests administered to other species (Cadieu, Cadieu, & Lauga, 1995; Moretti et al., 2015; Moscovice & Snowdon, 2006; Webster, Ward, & Hart, 2007). The presence of a hyaena littermate, in particular, significantly facilitated approach to the novel object, suggesting that littermates may have especially strong effects on juvenile hyaenas' confidence and propensity to explore new things.

Interestingly, individuals were more neophobic if they saw another individual contact the novel object, which is consistent with findings that a conspecific's presence or behaviour can inhibit approach to novel objects (Brown & Laland, 2002; Ryer & Olla, 1991; Stöwe, Bugnyar, Heinrich, & Kotrschal, 2006). In our test, this inhibitory effect may have been due to the tendency of juvenile hyaenas to startle or become skittish when others do. Juveniles are strongly influenced by the behaviour of their peers and it is common to see many cubs run into the communal den after a single cub startles. In our test, subjects often backed away or startled after contacting the novel object for the first time, so it seems possible that viewing this may have either inhibited other subjects from approaching at all or slowed their approach.

Notably, our study is one of only a few to directly relate personality traits to fitness in a wild mammal (Archard & Braithwaite, 2010). We found that boldness, but not neophobia or exploration, predicted survival to adulthood, with less bold individuals showing enhanced survivorship. These findings are consistent with a meta-analysis by Smith and Blumstein (2008), demonstrating that boldness consistently shows a significant negative correlation with survival across species. Furthermore, we found a negative relationship between boldness and juvenile survivorship regardless of disturbance, suggesting that the benefits of showing restraint in the face of risk accrue regardless of the level of human activity.

Differences in juvenile survivorship and predation pressure in the high- and low-disturbance areas may be shaping the differences we observed in juvenile boldness. When looking at hyaenas of all ages, Yoshida et al. (2016) found evidence for stabilizing selection with regard to boldness during lion–hyaena interactions, with reduced longevity for individuals who were either highly prone to take risks or who completely avoided them. However, we found that juveniles in high-disturbance areas were significantly less bold than juveniles in low-disturbance areas. Although surprising, this is probably due to decreased predation by lions in the high-disturbance area, where there has been a significant decline in lion densities and where juvenile survivorship was significantly greater than in the low-disturbance area from 2009 to 2013 (Green, 2015). This suggests that a reduction in predation pressure may be relaxing the selection pressure against shy individuals in the high-disturbance area.

Several questions should be answered by future research to make our results of the most use to applied carnivore conservation and the emerging field of conservation behaviour (Greggor et al., 2016). First, we must determine whether a juvenile's performance in our personality experiments predicts its behaviour and success in disturbed landscapes, particularly its likelihood of leaving protected areas, attacking livestock, or being killed by humans. Second, to determine whether juvenile personality traits remain stable into adulthood, we could measure these personality traits in individuals several times across the life span. We cannot assume stability in these traits beyond the juvenile period, as juvenile personality traits may represent adaptations specific to immature life stages (Bell & Stamps, 2004; Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013; Sinn, Gosling, & Moltschaniwskyj, 2008; Stamps & Groothuis, 2010).

Third, given our findings regarding boldness, disturbance and juvenile survivorship, it would be interesting to explore whether hyaena personality traits have fitness trade-offs over the lifetime of an individual, and whether such trade-offs differ between areas of high and low disturbance. In their meta-analysis, Smith and Blumstein (2008) found that, although bold individuals showed significantly lower survival, they also had higher reproductive success than less bold individuals. To test for such a trade-off in spotted hyaenas, we could relate boldness in the juveniles tested here to their future reproductive success. Furthermore, this would allow us to explore whether the fitness costs and benefits of boldness differ between areas of high and low disturbance, and whether disturbance may be acting as a selective pressure on the life history strategies of individuals inhabiting these areas.

Overall, our study not only reveals significant behavioural differences between animals in disturbed and pristine areas, but also raises important questions regarding how animals achieve behavioural adjustments in response to anthropogenic disturbance. Juvenile spotted hyaenas in both high- and low-disturbance areas are remarkably well buffered from direct human disturbance at their communal dens. Even juveniles living in areas that are generally disturbed by people are not directly bothered by people while they live at the den, and in fact they experience virtually no direct exposure at their dens to any anthropogenic activity, including livestock grazing. Therefore, it seems unlikely that human disturbance is directly shaping the behaviour of juveniles residing at the communal den. Nevertheless, the juveniles tested here showed marked disturbance-related behavioural variation very early in life. We are currently investigating the hypothesis that such behavioural differences are shaped indirectly, via maternal effects, as the behaviour and stress physiology of adult female spotted hyaenas can be greatly affected by human disturbance (Boydston et al., 2003; Kolowski & Holekamp, 2009; Van Meter et al., 2009). In many species, variation in maternal care or hormone exposure in utero shapes offspring personality, providing a potentially adaptive signal of environmental quality to offspring (Dantzer et al., 2013; Mateo & Maestripieri, 2009). In species that are long lived and slow growing, like spotted hyaenas, it may be that responding early in life to strong maternal signals of disturbance is critical to persistence in changing environments.

Acknowledgments

We thank the Kenyan National Commission for Science, Technology and Innovation, the Narok County Council, the Kenya Wildlife Service, and the Mara Conservancy for permission to conduct field research with hyaenas. We thank Wes Binder, David Green, Lily Johnson-Ulrich, Wilson Kilong, Charles Kolodziejski, Kevin McCormick, Jenna Parker and Benson Pion for assistance in the field. We also thank Andrew Dennhardt of Michigan State University's Center for Statistical Training and Consulting for guidance with statistical analysis and Lily Johnson-Ulrich for consultation about video coding. Finally, we thank Tom Getty, Joe Lonstein, Laura Smale and two anonymous referees for helpful comments on earlier drafts of the manuscript. This work was supported by National Science Foundation (NSF) Grants OISE 1556407 and DEB 1353110 to K.E.H., and by an NSF Graduate Research Fellowship to J.R.G. J.R.G. was also supported by fellowships from the College of Natural Sciences and the program in Ecology, Evolutionary Biology, and Behavior at Michigan State University. This work was made possible by support from the BEACON Center for the Study of Evolution in Action, funded by NSF grant OIA 0939454.

Supplementary material

Supplementary material associated with this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2017.08.023.

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