

Evolutionary Constraints on Equid Domestication: Comparison of Flight Initiation Distances of Wild Horses (*Equus caballus ferus*) and Plains Zebras (*Equus quagga*)

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Habituation to humans was an essential component of horse (*Equus caballus ferus*) domestication, with the nondomestication of zebras (*Equus quagga*) possibly reflecting an adaptive constraint on habituation. We present the human hunting hypothesis, arguing that ancestral humans hunted African animals, including zebras, long enough to promote a persistent wariness of humans, whereas a briefer period of hunting horses in Central Asia influenced by glacial cycles was unlikely to produce an equally persistent wariness. An alternative habituation to humans hypothesis, prompted by field observations, posits that zebras can habituate well to nonthreatening humans given sufficient exposure. If so, other factors must account for zebra nondomestication. To examine these hypotheses, we compared the flight initiation distances (FIDs) of wild horses in the United States and plains zebras in Africa to a human approaching on foot ($N = 87$). We compared the flight behavior of both species at sites with low and high exposure to humans (mean humans/acre = .004 and .209, respectively). Analyses revealed a significant interaction ($p = .0001$) between equid species and level of human exposure. The mean FIDs of horses (146 m) and zebras (105 m) with low human exposure did not differ appreciably ($p = .412$), but these distances were substantially longer ($p < .0001$) than those of horses (17 m) and zebras (37 m) with high human exposure that did differ significantly ($p < .0001$). The finding that plains zebras habituate less completely to humans than horses do might reflect an adaptive response to historical hunting and partly explain their resistance to domestication.

Keywords: flight initiation distance, habituation to humans, horse domestication, human hunting, plains zebras

The domestication of animals is a relatively recent, and relatively rare, phenomenon in the course of history. The lack of domesticated animals in sub-Saharan Africa might have simply been a nonoccurrence. With plentiful game, effective hunting tools, and a relatively low and stable human population level, there may have been no strong motive to domesticate any large ungulate species in the prevailing ecological and cultural milieu that included an abundant food supply (Cornish, 1908; Marlowe, 2005). On the other hand, the process of domestication might have been moderated by repeated interactions with nonthreatening humans or constrained by evolutionary factors associated with long-term hunting by humans. While elements such as diet specificity and social structure certainly played a role in the domestication pro-

cess, we focus herein on the role played by experiential and evolutionary factors.

Equidae as a Study System: Comparing Feral Horses and Plains Zebras

In an attempt to understand various factors underlying the domestication process, we compared the flight behavior from an approaching human of a formerly domesticated equid, the feral horse (*Equus caballus ferus*), and the never-domesticated plains zebra (*Equus quagga*). Measurement of a species' flight initiation distance (FID) to an approaching human (Blumstein, Anthony, Harcourt, & Ross, 2003; Sirot, 2010; Stankowich, 2008) is thought to reveal threat appraisal and flight distances remarkably similar to actual predatory encounters. Like other African ungulates, plains zebras are well adapted for maintaining safe distances from predators, such as lions (*Panthera leo*), or avoiding situations in which they could be overtaken when attacked (Creel, Schuette, & Christianson, 2014; Elliot, McTaggart Cowan, & Holling, 1977). Such behavior is apparent in Figure 1, which shows a young lioness stalking a small group of plains zebras in tall grass. Despite being detected, the lioness maintained her approach until the zebras trotted away with an FID of approximately 50 m.

There are several reasons that underlie our choice of comparing the FIDs of feral horses and plains zebras. Both species have a similar social structure and live in open habitats that vary in levels of exposure to humans. Like zebras, ancestral horses experienced

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Figure 1. (A) Two zebras exhibit alert postures after detecting an approaching lioness in the Ngorongoro Crater, Tanzania. (B) Seconds later the zebras trot away at flight initiation distances (FIDs) of approximately 50 m. Photographs by Richard Coss, 2013. See the online article for the color version of this figure.

relatively consistent predation from large felids (Burger et al., 2004; Stuart & Lister, 2011) prior to their presumed domestication on the Eurasian steppe approximately 5,500 years ago (Outram et al., 2009; Warmuth et al., 2012).

We considered for our study the inclusion of free-ranging Przewalski's horses (*Equus ferus przewalskii*), the closest living relative of the modern domestic horse (Orlando et al., 2013). The Przewalski's horse is a species rescued from the brink of extinction that underwent a genetic bottleneck, and some of the 12 founders were actually hybrids with domestic horses (Goto et al., 2011; Lau et al., 2009). Such hybridization makes it difficult to identify pure Przewalski's horses from hybrids, thereby making comparative research difficult to interpret.

There have been multiple documented attempts to domesticate various species of zebras in recent recorded history (Diamond, 2002). According to zookeepers and horse trainers, zebras have a distinct reputation for being aggressive and panicky, and this unpredictability makes them difficult to work with. Nevertheless, individual zebras have been successfully tamed and trained for riding and driving (see <https://www.youtube.com/watch?v=DHplnyWkqv0>). However, since domestication involves both human control of mating through selective breeding for at least a population of a given species (Clutton-Brock, 1992), as well as

establishing the ability to handle individuals relatively safely, it is clear that the zebra is not domesticated.

Free-living feral horses offer insight into how variable and context dependent the behaviors of an equid known to be domesticable, but not currently subject to artificial selection or direct management, can be. Feral horses become wary of humans who pose a threat via harassment or poaching but also habituate to nonthreatening humans once captured and started in an appropriate training program, a property making them tractable for adoption into private care.

Habituation Potential as a Prerequisite for Equid Domestication

Habituation is a form of nonassociative learning occurring with repeated exposure to salient environmental features without provocative consequences. This phenomenon is governed by inhibitory neural processes that progressively restrict behavioral expression (Shulgina, 2005). Short-term habituation can occur in specific situational contexts in which no meaningful consequences occur; that is, when there is no predictive change in the situation, such as browsing antelope periodically lifting their heads to monitor nearby resting lions. Long-term habituation to lions, however, would be maladaptive. For example, Stanley and Aspey (1984) documented persistent wariness of African ungulates over several months in a zoological park when lions were visible as they moved about in an adjacent enclosure. Habituation to humans also varies among species, and some species, such as Nyala antelope (*Nyala angasii*), are difficult to maintain in captive settings. When frightened by humans, they have been known to take flight in blind panic and crash into fences at fatally high speeds (Grandin & Deesing, 1998).

Intriguingly, there may be species differences as to how flexibly and adaptively feralized animals respond to humans in different contexts. For example, Reimers and colleagues (2012) showed that free-ranging feralized reindeer (*Rangifer tarandus*) with differing degrees of domestic ancestry varied in their vigilance and flight behaviors. Herds that were less related genetically to domestic herds were more vigilant and less approachable than herds more closely related to domestic herds, even though all the herds in the study experienced prolonged hunting.

Research Objectives

To gain insight into the possible interactive effects of habituation to humans and evolutionary constraints on habituation, we contrasted an experiential hypothesis involving the effects of different exposure to humans and an evolutionary hypothesis describing the historical role of human hunting. The comparison of two distinct hypotheses is consistent with Platt's (1964) recommendation for making a "strong inference" for only one hypothesis supported by experimental evidence.

Habituation to humans hypothesis. We formulated this hypothesis based on several relevant examples from the literature and anecdotes from field observations, which serve as evidence to suggest that zebras in the wild would have the potential to habituate to humans under the conducive conditions of no hunting or harassing interactions. A Tanzanian study of plains zebras' reactions to vehicular tourism showed that large differences can de-

velop in the FID of zebras in areas with high tourism and low threat of poaching versus areas with less tourism and greater threat of poaching (Nyahongo, 2008). Apparent zebra habituation to humans on horseback is also evident based on anecdotal observations by West Mmanoko, the lead guide from Limpopo Valley Horse Safaris. When the horse safari was first established in Botswana, it brought the first horses to the area. Zebras kept their distance, seeming to fear the horses as something new. After approximately 5–10 years, all the zebras in the region were notably more approachable, and those who lived closer to the stable and thus saw the horses frequently on the short ride itineraries were more approachable than other zebras that lived far away and were only exposed to horses when long rides went out. A converse to this pattern of wariness was reported by Levine and colleagues (2003), who observed Przewalski's horses standing "quite close" to humans on foot, yet would flee several kilometers from riders (who had historically hunted them). Importantly, since the horse-and-rider image template is the same, it stands to reason that these disparate, context-specific responses do not reflect an innate perception but rather a *learned* association about what a horse and rider signifies: in one context, safety; in the other, danger.

Finally, and most directly relevant to the present study, we report a vivid example of zebras habituating to humans on foot. The staff of the Zambezi Sun Hotel in Livingstone, Zambia, reported that they introduced free-ranging zebras to their predator-free grounds no earlier than 2004. Initially, zebras maintained a distance of approximately 10–20 m from humans, but after 3–4 years, zebras would allow humans to approach them to within touching distance. This is in sharp contrast to zebra behavior near another lodge near Lusaka, where zebras take flight at approximately 200 m at the mere sight of a vehicle.

Human hunting hypothesis. As originally hypothesized by Thuppil and Coss (2012), hunting was historically more consistent in eastern and southern Africa than in Asia, leading to the emergence of large mammalian prey that incorporated humans into their guild of predators. Effective antipredator behavior to human hunters likely accounts for sub-Saharan Africa experiencing the lowest extinction of megafauna, despite the longest occupation by human ancestors (Martin, 1966; Owen-Smith, 1987; Sandom, Faurby, Sandel, & Svenning, 2014) compared with geographic regions following dispersal from Africa where human hunters encountered human-naïve prey that were killed easily (Martin, 1984; Wroe, Field, Fullagar, & Jermin, 2004). According to this view, natural selection from hunting over many millennia led to the progressive wariness of approaching humans by prey, expressed by their adoption of larger flight distances. The difficulty of approaching wary prey by archaic humans and later anatomically modern humans precluded the utility of close-range thrusting spears employed around 500,000 years ago, prompting the adoption of forceful overhand spear throwing as early as 279,000 years ago (see Churchill & Rhodes, 2009; Roach, Venkadesan, Rainbow, & Lieberman, 2013; Sahle et al., 2013). As prey wariness progressed evolutionarily, further innovations involved the development of longer-range bows and arrows that first appeared in southern Africa 60,000–75,000 years ago, followed 50,000 years later by poisoned-arrow hunting (d'Errico et al., 2012; Lombard & Parsons, 2011). The frequency of zebra body parts transported and processed in South Africa around 60,000 years ago (Clark, 2011) indicated that modern humans were very effective hunters of Cape

zebras (*Equus capensis*), a species closely related to plains zebras (Orlando et al., 2009).

As a contemporary example of wariness to humans, Thompson's gazelles (*Gazella thomsoni*) have been observed to flee immediately once they detect a human in clear view (Walther, 1969, p. 188). However, when the human shape is masked by a vehicle, these antelope do not flee readily. To further bolster our argument of selective wariness of plains zebras toward humans and other zebra predators, but not nondangerous species, we have photographed plains zebras grazing inattentively in close proximity to individuals from 11 ungulate species, such as the larger Cape buffalo (*Syncerus caffer*; an incredibly dangerous species that will mob and kill humans), the blue wildebeest (*Connochaetes taurinus*), and olive baboons (*Papio anubis*).

The human hunting hypothesis emphasizes the different time scale and intensity of hunting horses and zebras based on fossil and cultural evidence for a much shorter absolute sympatry between horses and archaic humans (possibly as early as 280,000 years ago; see Reich et al., 2010) in Central Asia compared with ancestral humans and zebras in Africa, the latter spanning nearly 2 million years (Klein, 1999, p. 157). This difference in sympatry was primarily mediated by two circumstances: (a) the immigration of the early caballoid horse (*Equus scotti*) into Asia from North America more than 700,000 years ago that was already adapted to cool environments (Eisenmann, 1992) and (b) the dramatic climate fluctuations in Siberia and north-central Asia that likely precluded occupation by archaic humans (see Petit et al., 1999; Stewart & Stringer, 2012), but not cold-adapted horses during Ice Age conditions until this region was colonized by modern humans about 40,000–50,000 years ago (cf. Chlachula, 2010a, 2010b; Kuzmin, Kosintsev, Razhev, & Hodgins, 2009). Moreover, the open periglacial habitat in Central Asia suitable for horse grazing consisted of cold- and dry-adapted tundra-steppe grasslands and prostrate shrubs (Yurtsev, 2001) that afforded little cover for approaching hunters. Modern humans entering western Asia from Africa 40,000–50,000 years ago could compensate somewhat for hunting in an open habitat because they were equipped with plausible longer-range projectiles (Shea, 2006).

Modern humans hunted horses as soon as they were encountered in far southeast Europe (Prat et al., 2011), and horse hunting extended northward into the Arctic approximately 32,000 years ago (Pitulko et al., 2004) when temperatures during Marine Isotope Stage 3 were relatively warmer (Knies, Kleiber, Matthiessen, Müller, & Nowaczyk, 2001). Horses continued to be hunted during the Holocene in subarctic regions (Weber, Link, & Katzenberg, 2002) prior to and shortly following horse domestication in south-central Asia. Finally, it must be noted that the caballoid horse (*Equus ferus gallicus*) hunted by Neanderthals and modern humans in Europe (Niven, 2007) was not the ancestor of modern horses (Fronova, 2005; van Asperen, 2010). Thus, for comparing zebras with horses, the human hunting hypothesis is restricted in its scope to the historical hunting of modern horses from Central Asia that were eventually domesticated.

Experimental questions and predictions. The habituation to humans hypothesis predicts that both species, if frequently exposed to humans, will habituate equally well to humans by exhibiting equivalent FIDs. If zebras do habituate to the same degree as horses do under equivalent situations, this suggests that habituation

potential alone cannot account for different domestication outcomes.

Alternatively, the human hunting hypothesis proposes that the initial time frame of hunting horses in Central Asia consisted of intermittent sequences by archaic humans constrained by glacial cycles followed by consistently effective hunting by modern humans for no more than 40,000 years. Despite strong selection from hunting, this latter time frame is theorized as too brief in horses to engender the evolution of the complex perceptual and cognitive processes necessary for recognizing humans as potential predatory threats. As maladaptive as this possibility may seem, there are precedents. For example, the bearded pig (*Sus barbatus*) and barking deer (*Muntiacus muntjak*) were hunted persistently for about 40,000 years in Asia and still crop raid repeatedly despite harassment (Thuppil & Coss, 2012). In contrast, the longer duration of more consistent hunting by archaic and modern humans in Africa is theorized as sufficient to foster the evolution of this innate capability in plains zebras. The human hunting hypothesis also predicts that horses living in settings with low exposure to humans will respond to an approaching human on foot with a shorter FID than zebras with little exposure to humans. The human hunting hypothesis also predicts that horses frequently exposed to humans will allow much closer approaches than zebras frequently exposed to humans.

Method

Equids

We sought to empirically investigate how these two equids (the feral horse [*Equus caballus ferus*] and the plains zebra [*Equus quagga*]) would respond toward humans in contrasting contexts of high versus low exposure to humans. The experimenter (the first author) conducted FID tests at sites in North America and Africa selected for their high or low exposure to humans. Experimental procedures were conducted over three phases: July–September 2010 (Africa), June–July 2011 (United States), and August–December 2011 (Africa). The majority of the fieldwork was carried out in dry-season conditions, although the quality and abundance of forage varied somewhat due to factors such as proximity of water points, grazing conditions, and recency of last rains for any given FID test trial.

Wild horses. Wild horses are technically free-ranging feral horses. Feral horses are direct descendants of domestic *Equus caballus* that first arrived in North America with Spanish explorers in about 1500 A.D. The original, “purest” form of mustang (another term for feral horse) is thus of Spanish ancestry, but over the centuries various genes from cowboys’ Quarter horses, pioneers’ draft horses, and cavalry mounts were interwoven into the population, yielding a heterogeneous mixture of conformations, colors, and temperaments. Most individual feral horses can become so habituated to human observers that they have “virtually no flight distance” (Duncan, Harvey, & Wells, 1984; personal observations) and can successfully adapt to domestic life and become prized riding horses if captured and trained in a humane, species-appropriate manner. However, feral horses on the range, if threatened or frightened (such as when chased by humans in vehicles and/or shot at) can become extremely wary and cautious, running as soon as they detect humans either in vehicles or on foot from

distances of over 1 km (A. Dumas, personal communication, 2010, & C. C. Downer, personal communication, 2011). Because of this demonstrable high degree of behavioral plasticity, they are thus a natural reference category, providing a benchmark of comparison to assess other equids against.

We selected horse study sites that were not subject to routine “gathers” or roundups by the U.S. Bureau of Land Management or other wildlife management agencies to avoid any behavioral carryover effects from being chased by humans during these events. For low-exposure sites, we visited remote areas in Nevada near Highway 50, dubbed the “loneliest highway in America,” such as the Clan Alpine Range and Smith Creek Valley in Churchill County (39.60 N, 118.49 W) and Lyon County (38.95 N, 119.14 W), as well as Adobe Valley in Mono County, California (37.92 N, 118.95 W) near the California–Nevada border. For high-exposure sites, we visited suburbs of Reno, such as DaMonte Ranch (Washoe County; 40.56 N, 119.60 W), and nearby towns, such as Lockwood and Virginia Highlands in Storey County (39.41 N, 119.56 W). These sites contain bands of wild horses that are exposed to a high number of humans, where grassy areas such as front yards, schoolyards, and a meadow near a large residential neighborhood tend to attract horses, and activities such as gardening frequently cause residents to be on foot in sight of horses.

Plains zebras. Plains zebras are the iconic savannah-dwelling zebras found over a large expanse of sub-Saharan Africa. They are obligate grazers, needing access to grass and water daily. As nonruminants, they can survive well on coarse low-quality grass and are found in grasslands and wooded savannahs and from sea level to 3,500 m (Moehlman, 2002). In parts of their range, especially Tanzania and Kenya, they are known for combining with wildebeest and forming vast migratory herds. Their social structure consists of breeding groups (*harems* or *family bands*) and bachelor groups, and frequently multiple groups of both types will coalesce to form teeming herds. They will graze inattentively to nearby baboons and antelope.

Due to the in situ nature of this field experiment, it was not possible to fully standardize all high- and low-exposure sites to have the same densities of humans. We estimated the density of humans at a given site by dividing the approximate number of humans (residents and visitors) in the area by the acreage, if these data were available, and/or by referring to published population density estimates on maps for regions without definitive boundaries or known population numbers. Generally, the high-exposure sites were 1 order of magnitude more dense than the low-exposure sites, although the overall average density was .209 humans/acre for the high-exposure sites and .004 humans/acre for the low-exposure sites.

Truly remote sites with no human presence whatsoever, yet habitable by animals, are very rare in modern-day Africa, so we examined sites with relatively low exposure to humans instead. The greater relevance and ecological validity of sparsely populated versus entirely unpopulated sites is captured by a statement from a Tanzanian naturalist guide we worked with: “Wilderness is not an African concept” (R. Chekwaze, personal communication, 2010). We selected and accessed these sites with the assistance of local guides. Criteria for these sites included: few roads and buildings, no or low tourism, and no hunting allowed. These low-exposure sites were diverse, including public and private lands and community-managed protected areas in Kenya, Tanzania, Bo-

tswana, and South Africa. For high-exposure sites, we tested zebras in the Jejane Private Nature Reserve (Hoedspruit, South Africa) and the Mpala Research Centre (Nanyuki, Kenya). Opportunistically, we also conducted additional high-exposure trials while visiting the public walking trails in Mlilwane Wildlife Sanctuary (Mbabane, Swaziland).

Procedure

FID tests were conducted as one of the simplest and most cost-effective methods to quantify animals' fear of humans (Donadio & Buskirk, 2006; Tarlow & Blumstein, 2007). FID tests were performed on foot to horses or zebras by the experimenter after locating them (frequently with the assistance of a local guide) by vehicle or by hiking. A statistical comparison of vehicle and hiking contexts yielded no statistically reliable effect on FIDs. Approaches were only made to single equids or groups that were stationary, because if animals were already moving, it would have been ambiguous to ascribe changes in their speed or direction as responses to the human.

Each approach was made toward a selected "target" individual that was the closest individual to the experimenter. Although this method has a potential for bias, it provided a consistent decision rule for selecting targets. Unless there was any natural or inherent bias with age, sex, social rank, or other characteristic to cause unequal likelihoods of standing at the "front" of the group before a trial started, this rule would yield quasi-random sampling. Although there may be reason to predict that a band's stallion may position himself at the edge of his band, between its members and any potential dangers once he detected an ecologically meaningful agent of potential concern (see Dorn, 2009), the target was selected before any band members showed alert behaviors, so the danger of inadvertently sampling a majority of stallions was minimized.

Once a group of equids was located, the size of the group; proportions of juveniles and adults in the group; time of day; weather; vegetation density; and whether humans, other wildlife species, or livestock animals were in sight were recorded in a field notebook and verbally as commentary onto the video recording. The total distance to the target individual (start distance) was measured with the laser rangefinders Leupold RX-1000i (Beaverton, Oregon) or Bushnell Yardage Pro (Overland Park, Kansas) and recorded, and the approach trial began. The start point was marked by the vehicle or by leaving a backpack at the starting location. These FID approaches were video recorded using a Sanyo Xacti VPC-CG10 (Osaka, Japan) high-definition MPEG-4 video camera.

Dressed in natural hues, the experimenter walked directly toward the target at a rate of approximately one step per second (pace was guided by glancing at a digital wristwatch). Hard stares in the animals' direction or sustained direct eye contact with any individual were avoided (cf. Bateman & Fleming, 2011; Stankowich & Coss, 2007; Verrill & McDonnell, 2008).

The experimenter dropped a weighted flag to mark the location (alert point) when the target exhibited clear alert behavior (ceased grazing if it had been and assumed an *alert posture*). Alert posture is characterized by lifting the neck at a higher angle than a typical relaxed standing posture with head oriented to and ears and eyes directed toward the experimenter (Wathan & McComb, 2014; see Figure 1). Alert postures are sometimes accompanied by alarm

barks, snorts, or stamps. Despite this action, the experimenter continued the approach with as little alteration to the steady pace as possible.

When the target showed flight behavior (defined herein as deliberate locomotion at any gait, after alertness had been displayed, for two or more steps that increased the distance between the equid and the experimenter), the experimenter dropped a second weighted flag to mark the location (flight initiation point) and ceased approaching. Whether the target paused to orient toward and monitor the human during or after flight was also recorded. Alert distance and FID were calculated by measuring the distance from the alert point and the flight initiation point, respectively, from the start point and then subtracting each of those distances from the start distance (see Figure 2). We also quantified buffer distance, the distance between alertness and flight (Fernández-Juricic, Jimenez, & Lucas, 2001, 2002), that is directly comparable to other behavioral outcomes also measured in meters. Another relationship of interest we calculated was the ratio of FID to alert distance (Gulbrandsen, Segrist, del Castillo, & Blumstein, 2006).

Video coding. Videos were reviewed in real time, frame by frame, and coded jointly by teams of two trained research assistants working side by side to ensure real-time interrater reliability by consensus. Video coding allowed us to confirm the data recorded in the field notebook in real time and also to record additional behavioral data of interest. Such data included pausing to monitor the approaching experimenter and resuming relaxation, a behavioral state inferred by the resumption of any activity incompatible with flight or vigilance, such as grazing, social behavior, and autogrooming. We also noted the identities (target or nontarget) of the *first responders* in a group—that is, whether the target or another individual was the first to alert, and then which individual was the first to flee. There were thus several possible first-responder patterns for any given FID trial: (a) the target was first to alert and first to flee, (b) the target was first to alert but a nontarget individual was first to flee, (c) a nontarget individual was first to alert but the target was first to flee, (d) the same nontarget individual was first to alert and first to flee, or (e) two different nontarget individuals were first to alert and first to flee. Finally, vegetation density was categorized from the videos using an interval scale for three levels.

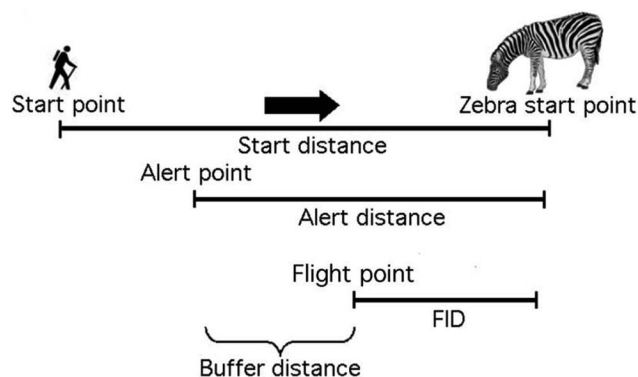


Figure 2. Schematic diagram depicting relationships between measurements of start distance, alert distance, buffer distance, and flight initiation distance (FID).

Data analyses. Statistical analyses were performed using Statistica (Statsoft) and JMP (Version 10). Each trial was classified into one of four categories that consisted of the various possible combinations of species and human exposure level: horse—low, horse—high, zebra—low, or zebra—high. Standardized effect sizes of mean differences (Cohen's d) were calculated for unequal numbers of animals using Equations 2 and 4 in Zakzanis (2001). Because specific effects were hypothesized for group differences, tests of simple effects were conducted in analyses of covariance irrespective of the statistical significance of main effects and interactions (see Winer, 1962, p. 208).

One zebra trial at a low-exposure site was discarded because it was determined to be a statistical outlier possibly related to a recent cheetah sighting in the area (for discussion of the effects of predators on zebra vigilance, see Creel et al., 2014). Statistical analyses were thus conducted on the following group sizes: horses—low = 12, horses—high = 12, zebras—low = 39, and zebras—high = 24.

Since start distance and alert distance are both potential constraints upon FID (Dumont, Pasquarella, Réale, Bogliani, & von Hardenberg, 2012), we compared the mean start distances and alert distances for all categories using two-factor analyses of variance. With the exception of the high-exposure category discussed below, all other category differences for start and alert distances were statistically significant ($\alpha = .05$). Since these measures were confounded with species, it was necessary to use them as centered covariates to statistically control their effects on species and human exposure comparisons. Additionally for these comparisons, all measures, with the exception of the ratio of FID to alert distance, were transformed to natural logarithms. While acknowledging Dumont and colleagues' (2012) point that start distance is an essentially arbitrary measure highly dependent on field logistics and that alert distance is generally a more behaviorally meaningful "starting point" for FID trials, we also propose that display of alertness is of interest in itself as a behavioral dependent variable. If two statistical models constructed using start or alert distance as covariates deliver the same overall pattern of results, the inclusion of analyses of alert distance as a response for models that use start distance as a covariate can be justified. Therefore, to incorporate these measures as covariates to control for their effects on buffer distance and FID, we centered start distance and alert distance for each category using deviations from their various means. The "many eyes and ears" theory of group formation (Lima, 1987) suggests that alertness to possible danger, although not necessarily more rapid flight response, would occur earlier in larger groups. Therefore, regression analyses examined the effect of herd size on alert distance and FID. Regression analyses were also conducted to examine the relationships between alert distance and FID and alert distance and buffer distance.

From the FID literature, we might also expect to see a consistent slope of approximately .44 for the ratio of FID to alert distance (Gulbransen et al., 2006). Moreover, there may be species and exposure differences in the distance between the FID and alert distance, and the alert distance and the buffer distance (Fernández-Juricic et al., 2002). As such, a possible correlation between alert distance and buffer distance would suggest an underlying syndrome of high alertness, correlating with a readiness to move and act without waiting very long for a potential threat to get much nearer (A. Sih, personal communication, 2011). Group size, proportion of juveniles, and vegetation density were also tested as possible predictors.

Results

Key continuous dependent behavioral variables were FID, alert distance, and buffer distance, which is the difference between the two, and the ratio of FID to alert distance. The means and 95% confidence intervals of these variables are shown in Table 1. Patterns of first-responder behavior are reported as percentages. Although all approaches were conducted with targets in clear view, vegetation density might alter risk assessment. A three-factor multinomial log-linear analysis with maximum likelihood estimation using species and human exposure as predictor variables examined the frequencies of the three vegetation density categories. The interaction approached statistical significance, likelihood ratio $\chi^2(2) = 5.6$, $p = .06$, a finding reflecting higher vegetation density in areas where both species had high exposure to humans. Neither the proportion of juveniles nor group size were found to exhibit reliable predictive properties to models of alert distance and FID.

Flight Initiation Distances

Comparisons of the FID for species and human exposure employed 2 two-factor analyses of covariance (ANCOVAs) of natural logarithms with either centered start distance/category or centered alert distance/category acting as covariates. These ANCOVAs revealed statistically significant interactions of species and human exposure with start distance as the covariate, $F(1, 82) = 20.442$, $p < .00005$, or alert distance as the covariate, $F(1, 82) = 24.586$, $p < .00001$. Tests of simple effects for both ANCOVAs revealed the sources of these interactions. The mean FIDs of horses and zebras from low-exposure categories (see Figure 3) did not differ significantly with start distance as the covariate ($p = .412$) or alert distance as the covariate ($p = .375$) with a medium effect size ($d = .64$). The mean FID of horses in the high-exposure category was reliably shorter with a large effect size ($d = .85$) than the mean FID of zebras in the high-exposure category—

Table 1
Mean Flight-Related Behaviors in Meters for Horses and Zebras in Categories With Low or High Exposure to Humans

Species and exposure level	Start distance	Alert distance	FID	Buffer distance	FID:alert ratio
Horse—low (12)	295.58 [207.1, 384.1]	199.58 [152.1, 247.1]	146.00 [91.6, 200.4]	53.58 [22.6, 84.6]	.76 [.59, .93]
Horse—high (12)	77.67 [38.0, 117.4]	49.33 [20.2, 78.5]	16.58 [8.9, 24.3]	27.92 [10.6, 45.2]	.26 [.17, .36]
Zebra—low (39)	193.31 [168.4, 218.3]	152.64 [134.3, 180.0]	105.41 [92.1, 118.7]	47.23 [33.0, 61.5]	.69 [.63, .75]
Zebra—high (24)	80.92 [50.7, 111.1]	61.83 [44.7, 79.0]	36.88 [25.9, 47.9]	25.42 [13.9, 37.0]	.56 [.45, .67]

Note. FID = flight initiation distance. Sample sizes appear in parentheses; 95% confidence intervals appear in brackets.

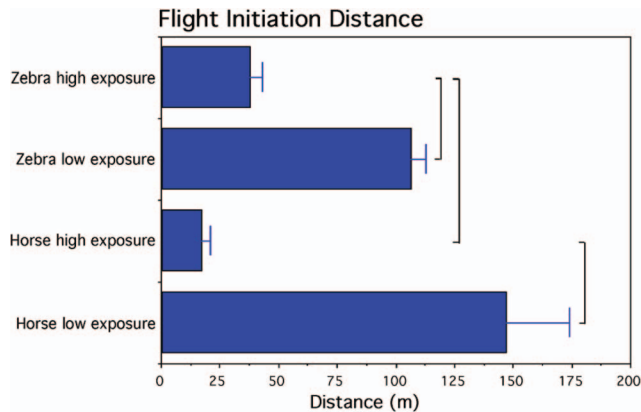


Figure 3. Mean flight initiation distances of horses and zebras at high and low levels of exposure to humans. Untransformed means and standard errors are shown. Vertical brackets depict statistically significant ($p < .0001$) differences indicated by ANCOVAs with either centered start distance or centered alert distance as covariates examining data transformed into natural logarithms. See the online article for the color version of this figure.

starting distance as the covariate: $F(1, 82) = 29.331, p < .00001$; alert distance as the covariate: $F(1, 82) = 35.407, p < .00001$. The mean FIDs of horses and zebras in the low-exposure categories were significantly longer, with large effect sizes ($d = 1.89$ and 1.83 , respectively), than the FIDs of their counterparts in the high-exposure categories—starting distance as the covariate: horses, $F(1, 82) = 97.412, p < .00001$; zebras, $F(1, 82) = 177.267, p < .00001$; alert distance as the covariate: horses, $F(1, 82) = 116.574, p < .00001$; zebras, $F(1, 82) = 59.988, p < .00001$.

Alert Distances

Alert distance is a behavioral response of interest in itself since it indicates awareness of a potential threat and the beginning of a decision process regarding the prey animal's response, as well as its relationship with subsequent flight. As mentioned above, horses and zebras at the high-exposure sites exhibited mean alert distances that did not differ appreciably. A two-factor ANCOVA on alert distances transformed to natural logarithms with centered start distance as the covariate revealed that, averaged for level of human exposure, mean alert distances were not significantly different between species (main effect: $p = .10$). Mean alert distances were markedly longer for horses and zebras in the low-exposure categories with large effect sizes ($d = 2.16$ and 1.71 , respectively) compared with their counterparts in the high-exposure categories—horse simple effect: $F(1, 82) = 174.655, p < .00001$; zebra simple effect: $F(1, 82) = 141.149, p < .00001$.

As revealed by regression analyses, the predictive relationships between alert distance and FID for each category (see Figure 4) were all statistically significant ($p < .0001$). Nevertheless, there was an exception to the consistency of the slope of this relationship between alert distance and FID across species and human exposure combinations. All combinations except the horse high-exposure category had slopes with overlapping 95% confidence intervals (CIs) and an overall slope of .69. The horse high-exposure cate-

gory had a significantly shallower slope (.26) to the relationship between alert distance and FID.

Buffer Distances

An ANCOVA with centered start distance as the covariate revealed that only the main effect for human exposure, averaged for species, was statistically significant, $F(1, 82) = 4.362, p < .05$. The source of this human exposure difference was restricted to the zebras in the low-exposure category that had a reliably longer buffer distance (see Table 1) with a medium effect size ($d = .55$) than zebras in the high-exposure category—simple effect: $F(1, 82) = 7.152, p < .01$. Contrary to the expectation arising from the study of birds by Fernández-Juricic and colleagues (2002), neither species nor human exposure level for three of the categories was a statistically reliable predictor. Regression analyses revealed that the predicted association between alert distance and buffer distance (see Figure 5) was statistically significant ($p < .0001$), except for horses at low-exposure sites ($p = .77$).

Ratio of FID to Alert Distance

The ratio of FID to alert distance assesses the proportional relationship of these measures of threat assessment (Gulbrandsen et al., 2006). A two-factor (species and exposure) analysis of variance (ANOVA) found that only the main effect of human exposure, averaged for species, was statistically significant, $F(1, 83) = 8.078, p < .01$. Tests of simple effects revealed that, after becoming alert, horses in the high-exposure category initiated flight after a reliably longer process of threat assessment (ratio of .563) than zebras (ratio of .354) in the high-exposure category, $F(1, 83) =$

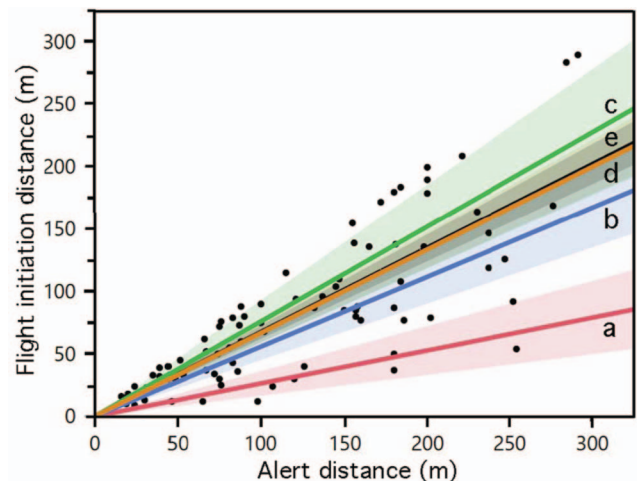


Figure 4. Association of flight initiation distance (FID) and alert distance. Slopes with 95% confidence intervals (shaded areas) reported in brackets are: (a) horse—high exposure = .26 [.17, .36], (c) horse—low exposure = .76 [.59, .93], (b) zebra—high exposure = .56 [.45, .67], (d) zebra—low exposure = .69 [.63, .75], and (e) overall slope shown as the black line superimposed on (d) = .69 [.63, .75]. Note. The slope confidence intervals for the horse high-exposure category (a) do not overlap the confidence intervals of the other categories. See the online article for the color version of this figure.

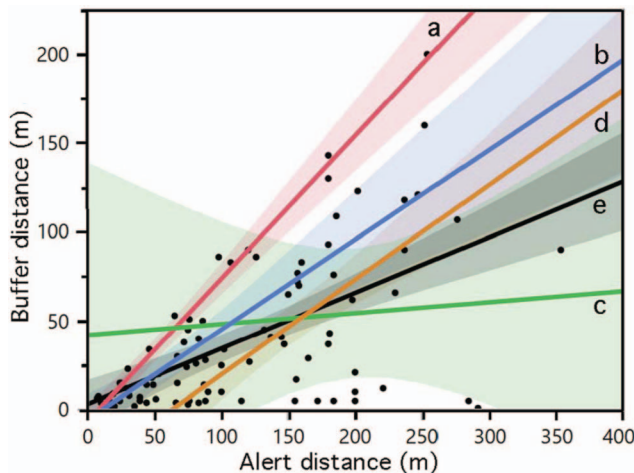


Figure 5. Association of alert distance and buffer distance. Slopes with 95% confidence intervals (shaded areas) reported in brackets are: (a) horse—high exposure = .81 [.68, .93], (c) horse—low exposure = .06 [−.40, .52], (d) zebra—high exposure = .51 [.32, .71], (b) zebra—low exposure = .45 [.28, .62], and (e) overall slope = .28 [.19, .37]. See the online article for the color version of this figure.

5.726, $p < .025$, $d = .76$, and horses (ratio of .299) in the low-exposure category, $F(1, 83) = 6.862$, $p = .01$, $d = .93$.

First Responders

Of all trials where the identity of the first alerter and the first to flee could be seen on video ($N = 71$), the target was the first to alert in 59% of trials and first to flee in 55% of trials. Overall, in only 45% of trials (38% of horses and 49% of zebras) was the first individual to become alert also the first individual to flee. This does not seem to represent a flighty behavioral syndrome (flighty temperament or arousability) since we would expect a much higher rate of consistency with the same individual being first to alert and also first to flee.

Discussion

The results of FID tests showed statistical findings that did not support all the theoretical attributes of the habituation to humans hypothesis or the human hunting hypothesis. Consistent with the habituation to humans hypothesis, when the effects of human exposure are compared, both species habituated reliably in settings where people could be seen routinely. Nevertheless, in support of the human hunting hypothesis, horses from high-exposure areas habituated more completely than zebras did from high-exposure areas, exhibiting a reliably shorter mean FID than zebras. However, the prediction from the human hunting hypothesis that horses from low-exposure areas would have a shorter mean FID than zebras from low-exposure areas was disconfirmed. Both horses and zebras perceived an approaching human as ecologically important, as evinced by their long FIDs that did not differ reliably. This finding is important because it suggests that a common history of predation on both species has engendered wariness of unfamiliar agents approaching with uncertain intent.

As manifested by their long FID and low ratio of FID to alert distance, reflecting a shorter period of threat assessment, it is clear that, despite domestication, feral horses in remote settings have not lost the keenness of their senses or the propensity to become alert and flee quickly to possible danger. It is not as clear whether they regard the human figure as a dangerous configuration or if they are merely engaging a parsimonious decision rule: A biological figure engaged in a slow looming approach is perceived as potentially dangerous.

Horses exhibited an exception to a general pattern found in relationships between alert distance and two other response variables—buffer distance and FID. It is very interesting to note that horses in the low-exposure category did not have a reliably predictable relationship between alert distance and buffer distance (although all other species–exposure level combinations did). In addition, horses at high exposure levels had a much shallower (and significantly different) slope of the regression line between alert distance and FID than any other species–exposure combination. This presents an interesting possible exception to Gulbrandsen's fixed slope rule, although since Gulbrandsen and colleagues (2006) did not specifically examine exposure level to humans as a factor in their research design, that could explain these differing patterns of findings.

The lesser degree of zebra habituation to humans compared with horses with high human exposure might have adaptive properties. Ethnoarchaeological observations of zebra hunting support this interpretation. For example, both 19th- and 20th-century anecdotes describe the successful hunting ranges of poisoned arrows shot by Hazda and San hunter–gatherers in eastern and southern Africa, respectively (cf. O'Connell, Hawkes, & Blurton Jones, 1988; Speth, 2010). Although arrows can travel up to 100 m, successful arrows are usually shot from 25- to 30-m distances that are just inside the average 37 m (95% CI = 26 to 48 m) FID for zebras from high-human-exposure areas. These effective arrow ranges are consistent with those described in experimental studies (reviewed by Hughes, 1998; Lombard & Phillipson, 2010). It is reasonable to argue that this coincidence of effective arrow range and zebra FID with high human exposure might reflect an adaptive response to poisoned-arrow hunting and minimally the 24,000-year time frame in which they have been used to kill large African prey (d'Errico et al., 2012). Thrown spears have even shorter effective ranges of 8–18 m (Lombard & Phillipson, 2010) and, in light of the much longer FIDs of horses and zebras with low human exposure, hunting would be particularly difficult in open habitats where humans would not have adequate cover. Such conditions might be circumvented by hunters adopting stealthy approaches, possibly using the skins of familiar animals as camouflage (Hughes, 1998).

Under circumstances we would expect to be conducive to habituation (high exposure to benign humans), a complementary explanation for why zebras from high-human-exposure areas did not habituate to as great a degree as horses in high-human-exposure areas did might reflect the occasional hunting of zebras even in no-hunting zones (for similar effects of hunting on the vigilance of other ungulates, see Benhaïem et al., 2008; Reimers, Loe, Eftestøl, Colman, & Dahle, 2009). In areas where local Africans have a taboo against hunting zebras, as in the case of the Maasai, we must remember that those taboos are not ironclad and were occasionally broken in times of very harsh conditions when livestock fared poorly. These intermittent hunts may have been

enough to maintain a functional level of wariness toward humans in the species as a whole, especially since an intermittent reinforcement schedule tends to yield long-lasting associative learning that resists behavioral extinction.

There are other behavioral attributes in addition to possible associative learning that might explain, in part, our evidence that zebras habituate less well to humans than horses. Zebras are known for being aggressive in social and antipredator defense contexts (Rubenstein, 2010), and there typically is an inverse correlation between aggression and plasticity (Koolhaas, Kato, Meerlo, Sgoifo, & de Boer, 1999; Sih, Bell, Johnson, & Ziemba, 2004; for exception in the African wild ass, see Marshall & Asa, 2013). According to authorities such as Rubenstein, 2010, aggression between male plains zebras is frequent and can be fierce; males often harass females, although the dominant stallion of a family band will attempt to protect them, and aggression between females is so rare that a single observed episode was felt to warrant a paper reporting it (Fischhoff et al., 2010). This strong difference is especially interesting in light of the genetic findings in domestic horses that indicate that one or a very small number of founder stallions (Warmuth et al., 2012), possibly chosen for an unusually docile temperament, appears to have given rise to all of today's population, while many mares contributed diverse haplotypes on the maternal side, indicating female wild stock being frequently introduced into the population (Lei et al., 2009). Such repeated introductions of wild females for breeding suggests that the earliest phase of horse domestication involved substantial habituation to humans. In contrast, captive breeding of plains zebras is very difficult (Lasley, Loskutoff, & Anderson, 1994), further supporting the argument that plains zebras might be adaptively constrained in habituating completely to humans, a process making them unmanageable for domestication.

Despite their domestic ancestry, feral horses provide an arguably equally good benchmark of natural caballoid behavior in the wild as Przewalski's horses, which themselves carry hybrid domestic ancestry, and some investigators even prefer feral horses as a reference (McGreevy, 2004). An interesting possible future direction for research into equid domestication could involve the ass division of the stenoid (zebra and ass) branch of the equid family tree. Studying behavioral differences between modern domestic donkeys and their ancestors, the Somali and/or Nubian wild ass, could theoretically yield fruitful insight; unfortunately, these rare equids are endemic to a currently dangerous area of the world.

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