Novelty Response of Wild African Apes to Camera-traps

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Summary

Temperament and personality research in humans and nonhuman animals measures behavioral variation in individual, population, or species-specific traits with implications for survival and fitness, such as social status, foraging and mating success [1–5]. Curiosity and risk-taking tendencies have been studied extensively across taxa by measuring boldness and exploration responses to experimental novelty exposure [3,4,6–15]. Here, we conduct a natural field experiment using wildlife monitoring technology to test variation in the reaction of wild great apes (43 groups of naïve chimpanzees, bonobos and western gorillas, across 14 field sites in Africa) to a novel object, the camera-trap. Bonobo and gorilla groups demonstrated a stronger looking impulse towards the camera-trap device compared to chimpanzees, suggesting higher visual attention and curiosity. Bonobos were also more likely to show alarm and other fearful behaviors, although such neophobic (and conversely, neophilic) responses were generally rare. Among all three species, individuals looked at cameras longer when they were young, were associating with fewer individuals, and did not live near a long-term research site. Overall, these findings partially validate results from great ape novelty paradigms in captivity [7,8]. We further suggest that species-typical leadership styles [16] and social and environmental effects, including familiarity with humans, best explain novelty responses of wild great apes. In sum, this study illustrates the feasibility of large-scale field experiments and the importance of both intrinsic and extrinsic factors in shaping animal curiosity.

Keywords: behavioral reaction, curiosity, exploration, *Gorilla gorilla*, looking time, neophobia, temperament, *Pan paniscus*, *Pan troglodytes*

Results and Discussion

Both environmental and social factors, such as group size, dominance status, habitat characteristics, and threats to survival, are critical for understanding variation in animal temperament and personality [1,2,5]. Consequently, we took advantage of a well-known wildlife monitoring method to investigate multiple social and ecological factors influencing neophobia and exploration in wild great apes. Recently, evidence for a 'captivity effect' was found for orang-utans [9,14], who avoid novelty almost entirely in the wild but not in captivity [9,14]. Such studies highlight the necessity for behavioral research in the wild for a more complete understanding of adaptive flexibility. Additionally, due to their close phylogenetic relationship to humans, data on great ape novelty responses may shed light on the selection pressures acting on temperament throughout hominin evolution [17].

Species dependent variation to novelty

The neophobia threshold (or adaptive flexibility) hypothesis predicts that animals benefit from neophilia (i.e., attraction to novelty) when they live in diverse habitats and are generalist foragers [3,18,19]. Chimpanzees live in more variable environments and have greater dietary breadth than either bonobos or gorillas, whose diets rely heavily on terrestrial herbaceous vegetation, a stable and predictable food resource [20]. Moreover, chimpanzees regularly engage in tool-use for extractive foraging, a skill that promotes behavioral innovation and is positively associated with exploration in many nonhuman primates and birds [3,6,9,12,21]. Therefore, we expect chimpanzees to be more neophilic than either bonobos or gorillas.

The self-domestication hypothesis proposes that as in many domesticated species, selection against aggression has resulted in bonobos having a less reactive temperament and increased social tolerance than other great apes [22]. Additionally, the leadership hypothesis, initially proposed for schools of fish [23], suggests that in species lacking a clear leader (i.e., egalitarian), individual personalities strongly predict group decisions about where to feed and rest [16,24]. The allocation of risk is predicted to be spread more evenly within the group in more egalitarian species, such as bonobos [25], rather than resting solely on one or a few, dominant individuals, as in gorillas and chimpanzees [26]. Captive experiments have shown that bonobos are more neophobic and risk-averse than chimpanzees or orang-utans, and exhibit novelty responses more similar to those of human children [7,8]. Therefore, we expect wild bonobos to be less reactive and more neophobic than other apes.

Species independent variation to novelty

An extension of the neophobia threshold hypothesis is the dangerous niche hypothesis, which predicts that individuals or social groups living in environments where they are regularly exposed to threats, such as hunting, will be more neophobic [3,11,19]. In the majority of studies to date, great apes were tested individually (but see [12]), even though individuals are more likely to take risks when in the presence of conspecifics [9,10,27], a phenomenon referred to as the risk-sharing or 'many eyes' hypothesis [28]. Studies on captive primates show young individuals often explore more than older individuals [12,15]. This likely reflects a greater need for young to learn about their social and ecological environment, which is facilitated by object exploration and play [15,29]. Similarly, humans also show a decrease in novelty seeking with age [29]. Finally, although ample evidence exists for sex differences in risk-taking behavior in humans [30], thus far, no evidence for sex differences in great ape exploratory behavior has been found using novelty experiments [7,12].

The goal of this study was to test the above-mentioned, non-mutually exclusive hypotheses in wild great apes encountering a novel object. To do so, we opportunistically collected 2,078 camera-trap video events of 43 social groups of wild great apes (13 chimpanzee, 7 bonobo and 23 western gorilla groups), from 14 different study sites across Equatorial Africa. These data came from 11 research sites of the Pan African Programme: the Cultured Chimpanzee [31] where chimpanzees and western gorillas were present, plus three additional bonobo field sites. To our knowledge, these camera-trap data represented the first time these apes were exposed to any autonomous monitoring device. Therefore, camera-traps represented novel objects for all great apes in this study and did not resemble any naturally occurring object in the wild. Given that the device and set-up of cameras was similar across all sites, reactions to these devices could be meaningfully compared across species, groups and individuals.

Camera-trap videos of apes were first screened for a possible reaction or "looking impulse", defined as an individual visibly orienting its face towards the camera-trap and looking at it, ([13]; Videos S1-S3). A looking impulse is a behavioral reaction measured in experimental paradigms of both children and animals to gauge visual exploration and infer curiosity towards a stimulus [13,32]. Once all videos containing a looking impulse were identified for each group (Table 1), we subsequently coded all camera reaction videos using a single ethogram: time spent looking at the device; time spent within 1m of the device; neophobic behaviors and neophilic behaviors (Table S1). At some sites, researchers knew individual apes while at others we used a combination of unique features to assign identities. Due to the difficulties in identifying all individuals observed on camera-trap videos, we first assessed looking impulse, or reaction to the device, at the group-level. For those individuals who exhibited looking impulses and crucially, could also be identified, we further conducted detailed individual-level analyses of their reactions (see STAR Methods).

In total, for all 43 great ape groups there were 611 camera-trap events where at least one individual exhibited a looking impulse (Table 1). Of these looking impulse events, 95 had at least one individual exhibiting a neophobic behavior and 104 had at least one individual exhibiting a neophilic behavior. Both a neophobic and neophilic response was observed in 26 of these 199 events, by the same (12 events) or different (14 events) individuals. We could confidently identify 275 individuals from all looking impulse videos, including 84 sexually mature (i.e., adolescent and adult) males, 114 mature females, and 77 young (i.e., infants and juveniles; Table S2). Identified individuals were observed reacting to camera-traps, on average, 1.66 times (range: 1-14 events per individual).

We conducted linear mixed models [33] for both group-level and individual-level analyses of great ape reactions to the camera-trap. We assessed whether each group ranged within 5 km of a long-term research site (y/n), and the number of human hunting signs encountered per kilometer of transect surveyed in the area (e.g., [34]). We included these variables to address the dangerous niche hypothesis, namely whether groups living near research sites were more neophilic whilst those living in areas with high hunting pressure were more neophobic. We also included the number of individuals present to test whether apes were more exploratory in the presence of others, as predicted by the risk-sharing hypothesis, as well as the age-sex class of the reactor for analyses of individual reactions. To account for potential habituation to camera-traps, we assigned an encounter sequence ID to all camera-trap events for each group. We also included the location of the camera-trap (path, food tree, tool-use site, or other), the travel direction of the individual before it exhibited the looking impulse (away, towards, or parallel), and event duration as control variables in our statistical models.

Group-level analyses in behavioral reactions

We calculated the proportion of camera-trap events where at least one individual of a group showed a clear looking impulse, out of the total number of camera-trap events for that group. Only one data point per group was used for this analysis, and we excluded groups that were only observed once on camera-traps. The proportion of camera-trap events with a looking impulse was significantly different among the three great apes (full-null model comparison: χ^2=17.65, df=5, P=0.003, N=36; Effect size: R^2_C=0.39; species: χ^2= 9.28, df=2, P=0.01; chimpanzee est ± SE: -0.49 ± 0.17, gorilla: -0.27 ± 0.16; Table 1) and no other predictor (long-term research site presence, average number of individuals present, and hunting pressure) had significant effects. The looking impulse was highest in bonobos and lowest in chimpanzees. Pairwise comparisons showed bonobos and gorillas did not differ from each other, but differed significantly from chimpanzees (Figure 1A).

We further examined all camera-trap events where a clear looking impulse occurred. We found no significant variation among species to come (or stay) within 1m of the device after looking at it (full-null model comparison: χ^2=8.01, df=5, P=0.16, N=31; R^2_C=0.33). To test for variation in neophilia and neophobia, we calculated the total number of events with at least one neophilic or neophobic behavior following a looking impulse by at least one individual out of the total number of camera reaction events for that group (Table 1). There was a significant species difference in neophobic behaviors (full-null model comparison: χ^2=14.20, df=5, P=0.014, N=31; R^2_C=0.38), with bonobos being more neophobic than both gorillas and chimpanzees (species: χ^2=10.86, df=2, P=0.004; chimpanzee est ± SE: -0.36± 0.10; gorilla: -0.30 ± 0.09; Figure 1B). Also, with greater human hunting pressure there were fewer neophobic responses to camera-traps (χ^2=7.27, df=1, P=0.007, est ± SE: -0.10 ± 0.03). However, the presence of long-term research sites did not have an effect. For neophilic reactions we found no significant variation explained by our predictors (full-null model comparison: χ^2=8.74, df=5, P=0.12, N=31; R^2_C=0.25).

Individual-level analyses in duration of behavioral reactions

For events where individuals showed a reaction to camera-traps and we could identify the group and the individual, we tested two additional quantitative measures of behavioral reactions to the device, namely looking time (i.e., the total duration an individual spent looking at the device) and the time spent within 1m of the camera-trap. No significant variation was found for time spent within 1m (full-null model comparison: χ^2=11.35, df=8, P=0.18, N=457; R^2_C=0.70). For looking time, there were no species differences, but age-sex class was significant (Table 2). Young individuals looked significantly longer at camera-traps compared to mature individuals, and mature females tended to look longer at camera-traps compared to mature males (Figure 2A). Additionally, great apes within the vicinity of a long-term research site had a shorter looking time compared to those that were more naïve to human researchers (Table 2 and Figure 2B).

Species differences in looking impulse and neophobic responses

The reactions of wild great ape to camera-traps suggest both intrinsic and extrinsic factors affect their behavioral reactions to novelty. Bonobos and gorillas were the most likely to react to camera-traps, with chimpanzees showing the least interest. This was in contrast to the neophobia threshold hypothesis where chimpanzees were predicted to be the most reactive and neophilic due to their more variable diet, proficiency in using tools, and greater range of habitat variation compared to either gorillas or bonobos. Moreover, in captivity chimpanzees often demonstrate risk-seeking behaviors and greater interest in novelty compared to bonobos and even humans [7]. In general, the low rate of responses observed in this study (Table 1) may have been due to insufficient interest in the camera-traps. Indeed, a novel object that elicits greater excitement or fear may have provoked a stronger behavioral response (e.g., a mirror [35]).

Bonobos were the most neophobic, supporting findings from captive studies which reveal negative responses towards novelty [7,8]. In contrast, gorillas and chimpanzees showed fewer neophobic behaviors. We tentatively propose that these results can be best explained by the leadership hypothesis [23,24,26]. The co-dominance between the sexes and high degree of female gregariousness in bonobos [25] may contribute to the lack of a defined leader and explain why bonobos were, on average, the most neophobic of the three great apes. A recent study on leadership in wild bonobos found multiple older females were central to group movement decisions [36]. Therefore, leadership in bonobos may be more shared among group members relative to chimpanzees and gorillas, where a socially dominant male may default as the leader [26]. However, more research on leadership strategies in great apes is needed to understand their relation to temperament and personality.

Under the self-domestication hypothesis, bonobos were predicted to be the least reactive [7,22]; however, they showed a strong looking impulse, similar to gorillas. In a recent comparison between domesticated dogs and wolves, wolves demonstrated greater interest in novel objects but also greater neophobia [10]. Therefore, contrary to predictions of the self-domestication hypothesis, bonobos reacted more like wolves than dogs to novel camera-traps. Together, these studies suggest that exploration tendency and neophobia may not always be negatively correlated. Likewise, curiosity may not always promote overt neophilia since animals can also obtain information about novel objects via more subtle behaviors, such as visual exploration, as measured in this study.

Individual differences in duration of visual exploration

We found no species differences with respect to the amount of time individuals spent looking at the camera-trap. In general, young individuals explored camera-traps for longer relative to mature males and females, confirming captive findings [6,12,15,37]. Similar to previous studies, we found limited evidence for a sex difference among mature individuals [7,9,12], although females tended to look longer. Additionally, we found that great apes accompanied by more individuals looked for a shorter duration at camera-traps. This may suggest that individuals risked being less vigilant when they were accompanied by more individuals, as predicted by the 'many eyes' hypothesis [28]. Likewise, past experience with humans, measured by the presence of long-term research sites, also shortened looking time, suggesting apes became desensitized to novelty. We also found a reduction in neophobic responses for groups living in areas with greater human hunting pressure, but no effect of hunting on individual looking time. Comparable results report reduced neophobia in spotted hyenas living in areas with high human disturbance [38]. Furthermore, apes may be protected by local 'taboos' [39] where they are not specifically targeted by hunters, permitting increased familiarity to novelty without a direct threat.

Overall, our results confirm findings from captive studies on great apes but also highlight the impact of natural socio-ecological settings on reactions to novelty. Great apes are often held as models for the last common ancestor between apes and hominins, particularly with respect to behavior [17]. Therefore, we suggest that ancestral hominins may have exhibited similar variation in neophobia and exploration which would have facilitated behavioral innovation and flexibility needed to adapt to changing environments throughout human evolution [7–9,14,27]. Moreover, any species differences in these traits would have been modulated by social and ecological parameters as observed in this study. However, given the limitations of our dataset with respect to control conditions and individual identification, we emphasize the need to replicate our group-level findings for individuals.

This research suggests that the dynamics of novelty responses and animal curiosity are more complex than previously understood. Importantly, all great apes are threatened in the wild and camera-trapping is a principal method for monitoring populations [31,40]. Our results suggest species-typical reactions and habituation to novelty should be considered when designing wildlife surveys, such as including a familiarization phase. Moreover, this study demonstrates how camera-traps and other technologies can be co-opted for field experiments to gain a better understanding of the adaptive nature of behavioral plasticity.

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Author Contributions

A.K.K and G.H. conceived the study; M.A., C.B., S.J.C., T.D., B.F., K.E.L., A.L.L., J.M., M.M.R., V.S., M.S., N.T., R.M.W. and H.S.K. organized and facilitated data collection; A.A., S.A., E.B., M.B., M.D., P.D., A-C.G., J.H., Y.A.K., G.M., S.M., J.v.S., and J.W. collected data in the field; A.K.K., G.H., M.A., M.S.M, M.B., G.B., M.D., P.D., J.H., Y.A.K., J.v.S., J.W., and H.S.K. conducted data processing and analyses; A.K.K. wrote the manuscript with contributions from all co-authors.

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Figure Titles & Legends

Figure 1. Group-level variation by species in A) the looking impulse, or reaction to, novel camera-trap devices and B) the tendency to show neophobic behavioral responses. Medians (*solid horizontal lines*) are shown for each species and model estimates (*dashed horizontal lines*) for each species when all other predictors are at their average value. The boxes represent quartiles with whiskers showing 2.5 and 97.5% percentiles and significance levels are indicated with asterisks ($P<0.05$=*; $P<0.01$= **; $P<0.001$=***). See also Figure S1, Table S3, Table S4, Video S1, Video S2 and Video S3.

Figure 2. Individual variation in looking time for 275 wild bonobos, chimpanzees and western gorillas by A) age-sex class and B) presence or absence of a long-term research site. For explanation, see Figure 1. See also Table S2.

Tables

Table 1. The total number of camera-trap events with a reaction, i.e., looking impulse, and subsequent behaviors coded for those reaction events, for 43 social groups of wild African great apes. Proportions provided in brackets for ease. See also Table S1, Figure S1, Table S4, Video S1, Video S2 and Video S3.

	# total events	CURIOSITY	NEOPHILIC		NEOPHOBIC		
		# looking impulse	# camera touch	# approach	# retreat	# startle	# alarm call or display
bonobo	119	97 (0.82)	3 (0.03)	14 (0.14)	15 (0.15)	16 (0.16)	7 (0.07)
chimpanzee	1867	461 (0.25)	61 (0.13)	36 (0.08)	30 (0.07)	39 (0.08)	14 (0.03)
gorilla	92	53 (0.58)	3 (0.06)	1 (0.02)	10 (0.19)	10 (0.19)	7 (0.13)
TOTAL	**2078**	**611**	**67**	**51**	**56**	**66**	**28**

Table 2. Linear Mixed Model results for total looking time per camera-trap reaction event for individually identified chimpanzees (179), bonobos (65) and western gorillas (31). Significant fixed effects have bold P values and confidence intervals (CIs). See also Table S2.

	Estimate ± SE	T	χ^2	df	P	CI 2.5%	CI 97.5%
Intercept	1.28 ± 0.39	3.31	-	-	-	0.73	2.46
Age-sex class_matureM	-0.22 ± 0.13	-1.71	8.66	2	**0.01**	**-0.47**	**0.02**
Age-sex class_young	0.30 ± 0.14	2.15				**0.04**	**0.58**
Species_chimpanzee	0.20 ± 0.32	0.63	0.53	2	0.77	-0.48	0.87
Species_gorilla	0.04 ± 0.37	0.11				-0.69	0.79
Encounter sequence ID	-0.02 ± 0.08	-0.25	0.05	1	0.82	-0.19	0.15
Number of individuals	-0.27 ± 0.09	-3.14	4.93	1	**0.03**	**-0.46**	**-0.09**
LT research site_yes	-0.48 ± 0.20	-2.41	4.88	1	**0.03**	**-0.90**	**-0.03**
Hunting pressure	0.15 ± 0.11	1.29	1.44	1	0.23	-0.08	0.37
Cam Location_other	0.22 ± 0.30	0.73	2.60	3	0.46	-0.46	0.90
Cam Location_path	0.13 ± 0.29	0.44				-0.47	0.74
Cam Location_tooluse	-0.22 ± 0.33	-0.67				-0.93	0.45
Travel direction_parallel	0.14 ± 0.16	0.89	0.74	2	0.69	-0.15	0.45
Travel direction_towards	0.08 ± 0.17	0.48				-0.23	0.41
Event duration	0.53 ± 0.07	7.06	18.60	1	**<0.001**	**0.36**	**0.68**

Full-null model comparison: $\chi2=16.98$, df=8, P=0.03, N=457; Effect size: $R^2_C=0.38$

STAR Methods

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Ammie K. Kalan (ammie_kalan@eva.mpg.de).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

All data were collected non-invasively in the field and consisted of indirect observations of wild *Pan troglodytes* ssp., *Pan paniscus*, and *Gorilla gorilla* ssp., collected solely via autonomous camera-trap devices, at fourteen field sites. Group, age-sex class and individual identification were assessed for each camera-trap video when possible (see Table S2 and Table S4 for the number of social groups and individuals identified at each field site). Permissions for the non-invasive data collection at each field site were provided by the relevant research, conservation and government authorities within each country. A complete list of authorities that granted field work permissions can be found in the Acknowledgements.

METHOD DETAILS

Camera-trap protocol in the field

The number of camera-traps used at each site was variable since study areas were variable in size and data were not collected at the same time at all sites. Cameras were set to record videos for 15 or 60 seconds when the infrared sensor was triggered by movement, white flash was never used. Black Bushnell Trophy camera-traps (models: 119435/119466) were used at all sites, except for Loango, to obtain video observations of wild apes. At Loango, brown Bushnell Trophy camera-traps (119776) and camouflage colored Scoutguard 550 Trail camera-traps were used. The Scoutguard 550 devices are similar in size, as well as lens and infrared sensor, to the Bushnell Trophy cameras (see Statistical analysis for how this source of variation was addressed). Cameras were at times protected within dark cases, especially during rainy seasons, but the front of the device always remained visible so as not to interfere with the sensor and lens. The devices were secured in the field when apes were not present, using dark plastic belts or cables wrapped around trees or branches, approximately at chest height. Camera-traps were installed at locations specifically chosen to increase detection of apes by targeting feeding trees ('food trees'), potential tool-use sites ('tool-use site'), natural bridges and trails ('path'), or forest clearings ('other'). Due to variation in openness and therefore visibility of the camera-trap at the different installation locations, we controlled for location type in our analyses. The cutting of vegetation around camera-traps was kept to the minimum required to ensure lenses were not obstructed. Further details of the camera-trapping protocol can be found at http://panafrican.eva.mpg.de/english/approaches_and_methods.php.

Coding of camera-trap videos

Camera-trap videos of chimpanzees and gorillas were watched and catalogued by members of the PanAf team and/or citizen scientists on the Chimp&See platform (www.chimpandsee.org) developed for the PanAf camera-trap data in collaboration with Zooniverse, to firstly identify which videos contained apes. Videos of chimpanzees were also screened for potential camera-trap reactions, i.e., a looking impulse, by these individuals. The proportion of videos with a looking impulse was quite low overall (611/ 2078 events; Table S4). More often than not, apes did not pass directly in front of the camera and they were also observed to have their attention elsewhere rather than on the camera-trap (e.g., see Video S1, Video S2 and Video S3 for the behavior of individuals before they look at the camera). Due to the limitations of using camera-trap videos to observe behavioral responses, we could not distinguish between individuals who knew the camera-trap was there and chose to ignore it, or those that did not notice it at all. This may account for the low number of observed reactions to the camera-trap.

Camera-trap videos of bonobos were watched by GH and his research team from LuiKotale and Salonga, and at Kokolopori by MS and his research team. AKK watched all bonobo and gorilla videos to find and code camera-trap reactions by individuals. AKK also calculated the number of individuals observed in an event, event duration, assessed camera location and identified groups and individuals when possible, often with the help of field researchers and by mapping coordinates of camera-traps. All gorilla groups were unhabituated to human observers. One bonobo site, Kokolopori, and one chimpanzee group, TaiEast, were habituated to human presence due to long-term research efforts; therefore individuals and groups could be easily identified [40]. Otherwise, identification of groups relied on cross-referencing the identification of individuals and their association with other individuals, across multiple camera-trap events. For Loango camera-trap data, gorilla and chimpanzee IDs had been previously determined for an ape abundance and ranging study [41]. For all other chimpanzee groups we assumed that one site represented a single chimpanzee group, also known as a community, although it is possible individuals of neighboring groups may have been caught on camera-traps as well. All individuals who looked at the camera-trap were assigned to an age-sex class [mature (adults and adolescents) males, mature females, and young (juveniles and infants of both sexes combined)]. Previous analyses by the PanAf have found high inter-observer agreement in the assignment of age-sex classes of individual apes from camera-trap videos, where AKK was one of the expert observers tested (Cohen's Kappa >0.8; PanAf, unpublished data).

Camera-trap events were defined as consecutive video clips from the same camera that were triggered within 15 minutes of each other, where individuals within an event can be counted and identified, similar to previous studies [42,43]. This interval has been validated to best reflect true party size estimates in chimpanzees therefore providing a reliable estimate of grouping patterns of wild apes [44]. AKK also watched all chimpanzee videos that were screened positively for a possible camera reaction to verify whether a looking impulse occurred, and if so (mean percentage correctly identified as looking impulse: 89% across six sites), coded the camera-reaction of those individuals and assessed or confirmed the camera location, the number of individuals observed and event durations that were calculated by her or the PanAf video coding team coordinated by MSM. For all three taxa, when a camera reaction was observed, we also noted the travel direction of the individual immediately before a looking impulse was observed as either away, towards or parallel to the camera-trap to control for variation in presentation of the novel object to each individual.

Videos where individuals were observed giving a looking impulse were subsequently watched and coded by AKK using the freeware BORIS [45]. Each video was re-watched at half speed, and each individual in the video was coded at a time, using an ethogram with detailed responses including looking time, and both neophobic and neophilic behaviors (Table S1). Behaviors were classified as either neophilic (affinity towards the novel object) or neophobic (alarm or affinity to move away from the novel object) based on the behavioral repertoire of the species and previous experimental research on great apes [7–9,12,14]. Of the 12 events where the same individual was observed emitting a neophobic and neophilic behavior, this was the combination of an approach and/or touch after being startled or alarm calling at the camera-trap. Only videos recorded at Loango did not have audio enabled but we did not see visual evidence of any reacting individual vocalizing (see also Statistical Analysis). BORIS time stamped all coded behaviors automatically and calculated durations for any state events, namely looking time and duration within 1m of the camera (Table S1).

We conducted an inter-observer reliability test for all behaviors of interest with an independent researcher who has experience watching chimpanzee camera-trap videos but was naïve to this ethogram. She recoded 120 videos taken from 120 different events comprising all three taxa and all sites. These 120 videos also included 50 videos with no looking impulse, to additionally test for the 'screening' process (see above). The independent coder used the same ethogram except call types were not tested, only the occurrence of a vocalization (Table S1), since it requires substantial training to be able to identify ape vocalization call types and AKK has this expertise. There was 96% agreement between the independent researcher and AKK for the type of behavior observed (Cohen's Kappa: K=0.96, P<0.0001, N=196) and the timing of these behaviors was highly similar (the difference between the timing of each behavior coded was significantly lower than expected by chance: P=0.001, N=166), calculated using a permutation test across a randomized sample of time lags with 1000 permutations.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses were conducted in R version 3.4.3 [46]. We conducted Linear Mixed Models at the group and individual-level where all LMMs [47] had a gaussian error structure with an identity link function and were fit using the function 'lmer' of the package lme4 with the argument REML set to false to obtain maximum likelihoods [48]. Group-level analyses were necessary to address the question as to whether there was variation across species in the tendency to react to camera-traps, i.e., exhibit a looking impulse, since it requires considering all camera-trap events where individuals of a group did, or did not, show a looking impulse. The group models were also used because all camera-trap events could be included, regardless of the visibility and identification of all individuals in a single video clip. This was particularly necessary for the neophilic and neophobic behaviors which occurred infrequently (Table 1 & Table S4) and could therefore not be fit using a poisson or binomial error structure due to underdispersion, instability and lack of convergence.

At the group-level, four LMMs were fitted, one for each of the four responses: proportion of camera-trap events per group where at least one individual showed a looking impulse, i.e., reacted to the device, proportion of camera-trap events with a reaction where at least one individual showed a neophilic response, proportion of camera-trap events with a reaction where at least one individual showed a neophobic response, and proportion of reaction events where at least one individual came within 1m of the camera after looking at it (see Figure 1 & Figure S1). All group-level LMMs had the same fixed and random effects structure. Fixed effects included species, presence of a long-term research site within 5 km of the group's territory or home range, the average number of individuals in the group seen in all camera-trap events (or in reaction events only) and human hunting pressure (encounter rate per kilometer walked of all hunting-related signs during transect surveys conducted within the vicinity of each social group). Human hunting pressure included the following signs: snares, empty cartridges, gunshots heard, poaching camps, and encountering poachers. We collected survey data from as close in time to the period of data collection as possible, but this was not always available for the exact time frame (e.g., Loango, Taï, and Kokolopori). Site was a random effect and the random slope for species within site was also included [49,50]. Note, all fixed effects were test predictors of interest and additional variables were not relevant at the group-level.

For all camera-trap reaction events where individuals could also be identified, we fit two LMMs, one for the total duration of looking time per individual in a camera reaction event, and another for the total duration of time spent within 1m of the camera after looking at it. For these two models the fixed effects included the test predictors species, long-term research site presence and human hunting pressure, as in the group-level analyses, but included three additional test predictors of age-sex class, event party size and event sequence ID. Multiple control variables were also included: event duration (log-transformed since responses were both log-transformed before fitting the models), location of the camera and travel direction of the individual. Random effects included camera ID, event ID, individual ID, group ID and site, with random slopes for all fixed effects within the levels of the random effects when it was necessary [49,50]. Due to the variation in camera-trap devices and lack of audio for the Loango dataset, in addition to including site as a random effect in all LMMs to account for site-specific variance in camera-trapping protocol [51], we further verified that removing Loango from the dataset did not significantly vary model estimates for any of the critical test predictors. Only for the individual-level analysis, the overall effect of age-sex class became non-significant if Loango was removed which was reflected in the pairwise comparison of mature males and mature females no longer being a trend; however, all other pairwise comparisons and model estimates did not change significance.

Before fitting any LMMs, covariates were z-transformed and factors were centered [52]. For all LMMs we also ensured that model assumptions were not violated by checking for normally distributed and homogeneous residuals using QQ-plots and plotting residuals against fitted values. We also verified that collinearity among predictors was not an issue by examining Variance Inflation Factors [53] using the function 'vif' of the package car on a linear model without random effects [54]. For all models, VIFs were between 1.02-1.38 and were therefore not an issue. We further verified model validity by checking that model estimates were stable when levels of the random effects were removed one at a time. To assess the significance of our predictors we first conducted a full versus null model comparison using a likelihood ratio test with the function 'anova' with a Chisq approximation [55]. Only if this was significant ($P<0.05$) did we go on to examine the significance of individual test predictors, also using likelihood ratio tests, using the function 'drop1' set to a Chisq approximation [33,49]. In those cases where a predictor was significant and it was a factor, we used the function 'glht' from the R package multcomp [56] for the model result, using a non-adjusted Tukey test to extract p-values for the pairwise comparison. Model confidence intervals were obtained using the built-in R function 'confint' and effect sizes were calculated using the function 'r.squaredGLMM' from the R package MuMIn [57] to obtain conditional effect sizes (R^2_C: variance explained by both the fixed and random effects of the model combined). Due to variation in sample size (N) for each model depending on the number of groups or camera-trap events included, we report N within the results upon first mention of the full versus null model comparisons.

KEY RESOURCES TABLE

Supplemental Information

Supplemental information includes 4 Tables, 1 Figure, 3 Videos.

Titles for Supplemental Videos

Video S1. A female bonobo (*Pan paniscus*) at Salonga National Park, DRC reacts to a camera-trap device (©PNS-Survey/Camera trap), Related to Figure 1, Table 1 and STAR Methods.

Video S2. Western gorillas (*Gorilla gorilla gorilla*) at LaBelgique, Cameroon react to a camera-trap device (©PanAf/MPI-EVA/PGS), Related to Figure 1, Table 1 and STAR Methods.

Video S3. West African chimpanzees (*Pan troglodytes verus*) at Kayan, Senegal react to a camera-trap device (©PanAf/MPI-EVA), Related to Figure 1, Table 1 and STAR Methods.