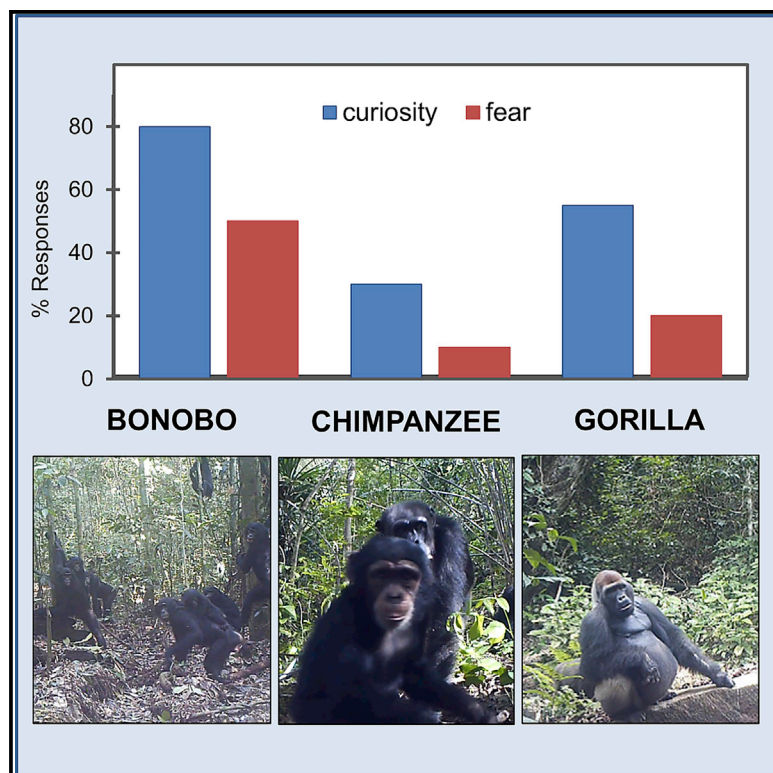


Current Biology

Novelty Response of Wild African Apes to Camera Traps

Graphical Abstract



Authors

Ammie K. Kalan, Gottfried Hohmann, Mimi Arandjelovic, ..., Jacob Willie, Roman M. Wittig, Hjalmar S. Kühl

Correspondence

ammie_kalan@eva.mpg.de

In Brief

Kalan et al. use a large-scale field experiment to assess the reaction of wild great apes toward a novel object: camera trap devices. Bonobos show the strongest looking impulse and are more neophobic than either gorillas or chimpanzees. Additional social and environmental effects on reactions demonstrate the complexities of animal curiosity.

Highlights

- Bonobos and gorillas had stronger looking impulses compared to chimpanzees
- Young apes looked longest at camera traps compared to mature individuals
- Presence of a research site or conspecifics reduced the duration of looking
- Both social and environmental factors affect great ape curiosity in the wild



Novelty Response of Wild African Apes to Camera Traps

Ammie K. Kalan,^{1,15,*} Gottfried Hohmann,¹ Mimi Arandjelovic,¹ Christophe Boesch,^{1,2} Maureen S. McCarthy,¹ Anthony Agbor,¹ Samuel Angedakin,¹ Emma Bailey,¹ Cosma Wilungula Balongelwa,³ Mattia Bessone,⁴ Gaëlle Bocksberger,¹ Sally Jewel Coxe,⁵ Tobias Deschner,¹ Marie-Lyne Després-Einspinner,¹ Paula Dieguez,¹ Barbara Fruth,^{6,7} Ilka Herbinger,⁸ Anne-Céline Granjon,¹ Josephine Head,¹ Yves Aka Kablan,^{1,2} Kevin E. Langergraber,⁹ Albert Lotana Lokasola,⁵ Giovanna Maretti,¹ Sergio Marrocoli,¹ Menard Mbende,¹⁰ Jennifer Moustgaard,⁵ Paul Kouame N'Goran,¹¹ Martha M. Robbins,¹ Joost van Schijndel,¹ Volker Sommer,¹² Martin Surbeck,^{1,5} Nikki Tagg,⁷ Jacob Willie,⁷ Roman M. Wittig,^{1,13} and Hjalmar S. Kühl^{1,14}

¹Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Deutscher Platz 6, 04103 Leipzig, Germany

²Wild Chimpanzee Foundation (WCF), Deutscher Platz 6, 04103 Leipzig, Germany

³Institut Congolais pour la Conservation de la Nature (ICCN), 13 Avenue des Cliniques, Kinshasa, Democratic Republic of the Congo

⁴Faculty of Biology/Department of Neurobiology, Ludwig Maximilians University of Munich, Großhaderner Straße 2, D-82152 Planegg-Martinsried, Germany

⁵Bonobo Conservation Initiative, 2701 Connecticut Ave. NW #702, Washington, DC 20008, USA

⁶School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool L3 3AF, UK

⁷Centre for Research and Conservation, Royal Zoological Society of Antwerp, B-2018 Antwerp, Belgium

⁸Department of Africa and South America, WWF Germany, Reinhardtstr. 18, 10117 Berlin, Germany

⁹School of Human Evolution and Social Change & Institute of Human Origins, Arizona State University, 900 Cady Mall, Tempe, AZ 85287, USA

¹⁰WWF in the Democratic Republic of the Congo (DRC), 14, Avenue Sergent Moke, Commune de Ngaliema, Kinshasa, Democratic Republic of the Congo

¹¹WWF Regional Office for Africa – Yaoundé Hub, PO Box 6776 Yaoundé, Cameroon

¹²Gashaka Primate Project, Nigeria c/o Department of Anthropology, University College London, London WC1H 0BW, UK

¹³Taï Chimpanzee Project, Centre Suisse de Recherches Scientifiques, BP 1301, Abidjan 01, Côte d'Ivoire

¹⁴German Centre for Integrative Biodiversity Research (iDiv) Halle-Leipzig-Jena, 04103 Leipzig, Germany

¹⁵Lead Contact

*Correspondence: ammie_kalan@eva.mpg.de

<https://doi.org/10.1016/j.cub.2019.02.024>

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 naive 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 toward 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.

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 orangutans, 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].



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

	# 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

Proportions provided in brackets for ease. See also [Figure S1](#), [Tables S1](#) and [S4](#), and [Videos S1](#), [S2](#), and [S3](#).

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 expected 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 orangutans and exhibit novelty responses more similar to those of human children [7, 8]. Therefore, we expected 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 that 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 both 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 setup 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 toward 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 toward 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 1 m of the device, and 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)

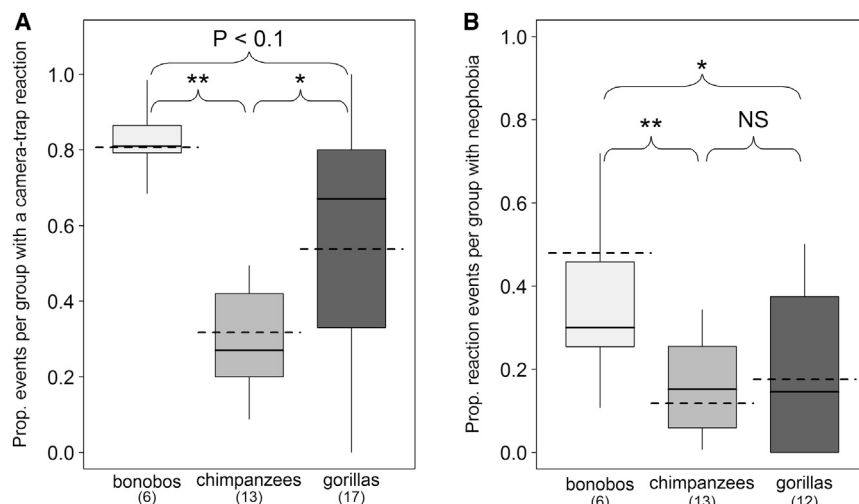


Figure 1. Group-Level Variation by Species in the Looking Impulse and Neophobic Response to Novel Camera Trap Devices

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](#), [Tables S3](#) and [S4](#), and [Videos S1](#), [S2](#), and [S3](#).

gorillas did not differ from each other but differed significantly from chimpanzees ([Figure 1A](#)).

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 while 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, toward, 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: $\chi^2 = 17.65$, $df = 5$, $p = 0.003$, $n = 36$; effect size: $R^2_C = 0.39$; species: $\chi^2 = 9.28$, $df = 2$, $p = 0.01$; chimpanzee $est \pm SE$: -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 or hunting pressure) had significant effects. The looking impulse was highest in bonobos and lowest in chimpanzees. Pairwise comparisons showed that bonobos and

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 1 m of the device after looking at it (full null model comparison: $\chi^2 = 8.01$, $df = 5$, $p = 0.16$, $n = 31$; $R^2_C = 0.33$). 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: $\chi^2 = 14.20$, $df = 5$, $p = 0.014$, $n = 31$; $R^2_C = 0.38$), with bonobos being more neophobic than both gorillas and chimpanzees (species: $\chi^2 = 10.86$, $df = 2$, $p = 0.004$; chimpanzee $est \pm SE$: -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 ($\chi^2 = 7.27$, $df = 1$, $p = 0.007$, $est \pm SE$: -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: $\chi^2 = 8.74$, $df = 5$, $p = 0.12$, $n = 31$; $R^2_C = 0.25$).

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 1 m of the camera trap. No significant variation was found for time spent within 1 m (full null model comparison: $\chi^2 = 11.35$, $df = 8$, $p = 0.18$, $n = 457$; $R^2_C = 0.70$). 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 naive to human researchers ([Table 2](#); [Figure 2B](#)).

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)

	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_toward	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

Significant fixed effects have bold p values and confidence intervals (CIs). See also [Table S2](#).

Full-null model comparison: $\chi^2 = 16.98$, $df = 8$, $p = 0.03$, $n = 457$; effect size: $R^2_C = 0.38$

Species Differences in Looking Impulse and Neophobic Responses

The reactions of wild great apes to camera traps suggest that 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 also 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 that reveal negative responses toward 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 that 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 that 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.

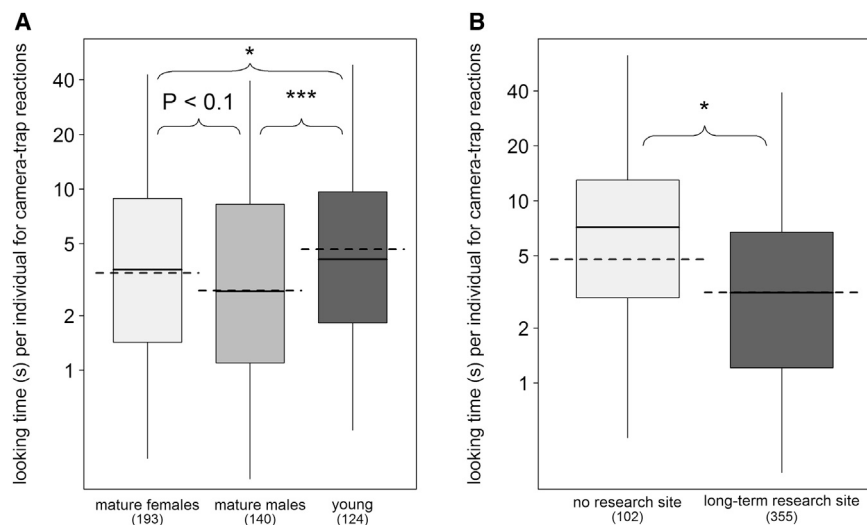


Figure 2. Looking Time Variation for Individually Identified Chimpanzees, Bonobos, and Western Gorillas

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.

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 that 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 that 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 animal behavioral plasticity.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
 - Camera-trap protocol in the field
 - Coding of camera-trap videos
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental Information can be found with this article online at <https://doi.org/10.1016/j.cub.2019.02.024>.

A video abstract is available at <https://doi.org/10.1016/j.cub.2019.02.024#mmc6>.

ACKNOWLEDGMENTS

This work was funded by the Max Planck Society, Max Planck Society Innovation Fund, and Heinz L. Krekeler Foundation, and data related to the Salonga National Park in the Democratic Republic of the Congo was funded by the Kreditanstalt für Wiederaufbau (KfW Group) on behalf of the German Government and WWF Germany. We sincerely thank Karsten Dierks, Henk Eshuis, Veerle Hermans, Sonja Nicholl, Luc Tédonzong, and Rodolphe Violleau for assistance in the field; Andrew Dunn, John Hart, Martin Ter Heegde, Thurston Cleveland Hicks, and Inaoyom Imong for facilitating field work; Chimp&See citizen scientists for help with video coding for multiple PanAf sites (<https://www.chimpandsee.org/#/about/authors>); Kristin Haverkamp, Stefano Lucchesi, Anna Preis, Liran Samuni, and Claudia Wilke for help with the identification of individuals; and Vittoria Estienne for her participation in the interobserver reliability test. We also thank the following wildlife and government authorities for permissions to conduct and host research sites in their countries: Ministère de la Recherche Scientifique et de l'Innovation, Ministère des Forêts et de la Faune in Cameroon, Ministère de la Recherche Scientifique, and Ministère des Eaux et Forêts in Côte d'Ivoire; Institut Congolais pour la Conservation de la Nature and Ministère de la Recherche Scientifique in DR Congo; Agence Nationale des Parcs Nationaux, Centre National de la Recherche Scientifique et Technologique, and Société Equatoriale d'Exploitation Forestière in Gabon; Ministère de l'Agriculture de l'Élevage et des Eaux et Forêts in Guinea; Instituto da Biodiversidade e das Áreas Protegidas in Guinea-Bissau; Forestry Development Authority in Liberia; National Park Service and Conservation Society of Mbe Mountains in Nigeria; Direction des Eaux, Forêts Chasses et de la Conservation des Sols, and Réserve Naturelle Communautaire de Dindéfelo in Senegal; and Uganda National Council for Science and Technology, Uganda Wildlife Authority in Uganda. We also thank three anonymous reviewers for their feedback, which significantly improved this manuscript.

AUTHOR CONTRIBUTIONS

A.K.K. and G.H. conceived the study; M.A., C.B., C.W.B., S.J.C., T.D., B.F., I.H., K.E.L., A.L.L., M.M., J.M., P.K.N., 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.-L.D.-E., 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.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: September 18, 2018

Revised: December 19, 2018

Accepted: February 6, 2019

Published: March 14, 2019

REFERENCES

- Réale, D., Reader, S.M., Sol, D., McDougall, P.T., and Dingemanse, N.J. (2007). Integrating animal temperament within ecology and evolution. *Biol. Rev. Camb. Philos. Soc.* **82**, 291–318.
- Sloan Wilson, D., Clark, A.B., Coleman, K., and Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **9**, 442–446.
- Greenberg, R., and Mettke-hofmann, C. (2001). Ecological aspects of neophobia and neophilia in birds. In *Current Ornithology*, V. Nolan, Jr., and C.F. Thompson, eds. (Springer), pp. 119–178.
- Kurvers, R.H.J.M., Prins, H.H.T., van Wieren, S.E., van Oers, K., Nolet, B.A., and Ydenberg, R.C. (2010). The effect of personality on social foraging: shy barnacle geese scrounge more. *Proc. Biol. Sci.* **277**, 601–608.
- Sih, A., Bell, A., and Johnson, J.C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**, 372–378.
- Biondi, L.M., Bó, M.S., and Vassallo, A.I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*). *Anim. Cogn.* **13**, 701–710.
- Herrmann, E., Hare, B., Cissewski, J., and Tomasello, M. (2011). A comparison of temperament in nonhuman apes and human infants. *Dev. Sci.* **14**, 1393–1405.
- Heilbronner, S.R., Rosati, A.G., Stevens, J.R., Hare, B., and Hauser, M.D. (2008). A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biol. Lett.* **4**, 246–249.
- Damerius, L.A., Graber, S.M., Willems, E.P., and van Schaik, C.P. (2017). Curiosity boosts orang-utan problem-solving ability. *Anim. Behav.* **134**, 57–70.
- Moretti, L., Hentrup, M., Kotschal, K., and Range, F. (2015). The influence of relationships on neophobia and exploration in wolves and dogs. *Anim. Behav.* **107**, 159–173.
- Brown, G.E., Ferrari, M.C.O., Elvidge, C.K., Ramnarine, I., and Chivers, D.P. (2013). Phenotypically plastic neophobia: a response to variable predation risk. *Proc. Biol. Sci.* **280**, 20122712.
- Massen, J.J.M., Antonides, A., Arnold, A.-M.K., Bionda, T., and Koski, S.E. (2013). A behavioral view on chimpanzee personality: exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. *Am. J. Primatol.* **75**, 947–958.
- Berlyne, D.E. (1966). Curiosity and exploration. *Science* **153**, 25–33.
- Forss, S.I.F., Schuppli, C., Haiden, D., Zweifel, N., and van Schaik, C.P. (2015). Contrasting responses to novelty by wild and captive orangutans. *Am. J. Primatol.* **77**, 1109–1121.
- Visalberghi, E., Janson, C.H., and Agostini, I. (2003). Response toward novel foods and novel objects in wild *Cebus apella*. *Int. J. Primatol.* **24**, 653–675.
- King, A.J., Johnson, D.D.P., and Van Vugt, M. (2009). The origins and evolution of leadership. *Curr. Biol.* **19**, R911–R916.
- Duda, P., and Zrzavý, J. (2013). Evolution of life history and behavior in Hominidae: towards phylogenetic reconstruction of the chimpanzee-human last common ancestor. *J. Hum. Evol.* **65**, 424–446.
- Wright, T.F., Eberhard, J.R., Hobson, E.A., Avery, M.L., and Russello, M.A. (2010). Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. *Ethol. Ecol. Amp Evol.* **22**, 393–404.
- Greenberg, R. (1990). Ecological plasticity, neophobia, and resource use in birds. *Stud. Avian Biol.* **13**, 431–437.
- Hohmann, G., Robbins, M.M., and Boesch, C. (2006). *Feeding Ecology in Apes and Other Primates* (Cambridge University Press).
- Lefebvre, L., Reader, S.M., and Sol, D. (2004). Brains, innovations and evolution in birds and primates. *Brain Behav. Evol.* **63**, 233–246.
- Hare, B., Wobber, V., and Wrangham, R. (2012). The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Anim. Behav.* **83**, 573–585.
- Levin, L.E. (1996). Passage order through different pathways in groups of schooling fish, and the diversified leadership hypothesis. *Behav. Processes* **37**, 1–8.
- Kurvers, R.H.J.M., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S.E., Ydenberg, R.C., and Prins, H.H.T. (2009). Personality differences explain leadership in barnacle geese. *Anim. Behav.* **78**, 447–453.
- Surbeck, M., Girard-Buttoz, C., Boesch, C., Crockford, C., Fruth, B., Hohmann, G., Langergraber, K.E., Zuberbühler, K., Wittig, R.M., and Mundry, R. (2017). Sex-specific association patterns in bonobos and chimpanzees reflect species differences in cooperation. *R. Soc. Open Sci.* **4**, 161081.
- Boinski, S., and Garber, P., eds. (2000). *On the Move: How and Why Animals Travel in Groups* (Chicago, IL: University of Chicago Press).
- Rosati, A.G., and Hare, B. (2012). Decision making across social contexts: competition increases preferences for risk in chimpanzees and bonobos. *Anim. Behav.* **84**, 869–879.
- Pulliam, H.R. (1973). On the advantages of flocking. *J. Theor. Biol.* **38**, 419–422.
- Lucas, R.E., and Donnellan, M.B. (2011). Personality development across the life span: longitudinal analyses with a national sample from Germany. *J. Pers. Soc. Psychol.* **101**, 847–861.
- Byrnes, J.P., Miller, D.C., and Schafer, W.D. (1999). Gender differences in risk taking: A meta-analysis. *Psychol. Bull.* **125**, 367–383.
- Kühl, H.S., Kalan, A.K., Arandjelovic, M., Aubert, F., D'Auvergne, L., Goedmakers, A., Jones, S., Kehoe, L., Regnaut, S., Tickle, A., et al. (2016). Chimpanzee accumulative stone throwing. *Sci. Rep.* **6**, 22219.
- Haude, R.H., Graber, J.G., and Farres, A.G. (1976). Visual observing by rhesus monkeys: some relationships with social dominance rank. *Anim. Learn. Behav.* **4**, 163–166.
- Dobson, A.J., and Barnett, A. (2008). *An Introduction to Generalized Linear Models, Third Edition* (Boca Raton, FL: Chapman and Hall/CRC).
- Kablan, Y.A., Diarrassouba, A., Mundry, R., Campbell, G., Normand, E., Kühl, H.S., Koné, I., and Boesch, C. (2017). Effects of anti-poaching patrols on the distribution of large mammals in Taï National Park, Côte d'Ivoire. *Oryx*. <https://doi.org/10.1017/S0030605317001272>.
- Anderson, J.R., Hubert-Brierre, X., and McGrew, W.C. (2017). Reflections in the rainforest: full-length mirrors facilitate behavioral observations of unhabituated, wild chimpanzees. *Primates* **58**, 51–61.
- Tokuyama, N., and Furuichi, T. (2017). Leadership of old females in collective departures in wild bonobos (*Pan paniscus*) at Wamba. *Behav. Ecol. Sociobiol.* **71**, <https://doi.org/10.1007/s00265-017-2277-5>.
- Almeling, L., Hammerschmidt, K., Sennhenn-Reulen, H., Freund, A.M., and Fischer, J. (2016). Motivational shifts in aging monkeys and the origins of social selectivity. *Curr. Biol.* **26**, 1744–1749.
- Greenberg, J.R., and Holekamp, K.E. (2017). Human disturbance affects personality development in a wild carnivore. *Anim. Behav.* **132**, 303–312.

39. Boesch, L., Mundry, R., Kühl, H., and Berger, R. (2017). Wild mammals as economic goods and implications for their conservation. *Ecol. Soc.* 22, <https://doi.org/10.5751/ES-09516-220436>.
40. Després-Einspinner, M.-L., Howe, E.J., Drapeau, P., and Kühl, H.S. (2017). An empirical evaluation of camera trapping and spatially explicit capture-recapture models for estimating chimpanzee density. *Am. J. Primatol.* 79, e22647.
41. Head, J.S., Boesch, C., Robbins, M.M., Rabanal, L.I., Makaga, L., and Kühl, H.S. (2013). Effective sociodemographic population assessment of elusive species in ecology and conservation management. *Ecol. Evol.* 3, 2903–2916.
42. Boesch, C., Kalan, A.K., Agbor, A., Arandjelovic, M., Dieguez, P., Lapeyre, V., and Kühl, H.S. (2017). Chimpanzees routinely fish for algae with tools during the dry season in Bakoun, Guinea. *Am. J. Primatol.* 79, 1–7.
43. Tagg, N., McCarthy, M., Dieguez, P., Bocksberger, G., Willie, J., Mundry, R., Stewart, F., Arandjelovic, M., Widness, J., Landsmann, A., et al. (2018). Nocturnal activity in wild chimpanzees (*Pan troglodytes*): Evidence for flexible sleeping patterns and insights into human evolution. *Am. J. Phys. Anthropol.* 166, 510–529.
44. McCarthy, M.S., Després-Einspinner, M.-L., Samuni, L., Mundry, R., Lemoine, S., Preis, A., Wittig, R.M., Boesch, C., and Kühl, H.S. (2018). An assessment of the efficacy of camera traps for studying demographic composition and variation in chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* 80, e22904.
45. Friard, O., and Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol.* 7, 1325–1330.
46. R Development Core Team (2017). R: A language and environment for statistical computing (R Foundation for Statistical Computing).
47. Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48.
48. Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., et al. (2016). lme4: Linear Mixed-Effects Models using “Eigen” and S4. Available at: <https://cran.r-project.org/web/packages/lme4/index.html> [Accessed December 2, 2016].
49. Barr, D.J., Levy, R., Scheepers, C., and Tily, H.J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *J. Mem. Lang.* 68, 255–278.
50. Schielzeth, H., and Forstmeier, W. (2009). Conclusions beyond support: overconfident estimates in mixed models. *Behav. Ecol.* 20, 416–420.
51. Laird, N.M. (2004). *Analysis of Longitudinal and Cluster-correlated Data* (Beachwood, OH: IMS).
52. Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* 1, 103–113.
53. Bowerman, B.L., and O’Connell, R. (2000). *Linear Statistical Models: An Applied Approach, Second Edition* (Belmont, CA: Duxbury Press).
54. Fox, J., and Weisberg, H.S. (2001). *An R Companion to Applied Regression Revised* (Thousand Oaks, CA: Sage Pubn).
55. Forstmeier, W., and Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner’s curse. *Behav. Ecol. Sociobiol. (Print)* 65, 47–55.
56. Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A., and Scheibe, S. (2017). multcomp: Simultaneous Inference in General Parametric Models. Available at: <https://cran.r-project.org/web/packages/multcomp/multcomp.pdf> [Accessed June 27, 2018].
57. Bartoń, K. (2018). MuMIn: Multi-Model Inference. Available at: <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf> [Accessed June 27, 2018].

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
<i>Pan troglodytes verus</i>	Bakoun, Guinea; Grebo, Liberia; Kayan, Senegal & Taï, Côte d'Ivoire	N/A
<i>Pan troglodytes troglodytes</i>	Campo Maan, Cameroon & Loango, Gabon	N/A
<i>Pan troglodytes schweinfurthii</i>	Bili, DRC & Ngogo, Uganda	N/A
<i>Pan troglodytes ellioti</i>	Gashaka, Nigeria	
<i>Pan paniscus</i>	Kokolopori, LuiKotale, & Salonga, DRC	N/A
<i>Gorilla gorilla gorilla</i>	Campo Maan, Cameroon; La Belgique, Cameroon; Loango, Gabon	N/A
<i>Gorilla gorilla diehli</i>	Mbe, Nigeria	N/A

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 [Tables S2](#) and [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 Acknowledgments.

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 s 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 cataloged by members of the PanAf team and/or citizen scientists on the Chimp&See platform (<https://www.chimpandsee.org>) developed for the PanAf camera-trap data in collaboration with Zooniverse, to first 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 min 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, toward 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 free-ware 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 toward 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 1 m 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 naive 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 1 m 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 1 m 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.