



## Influence of live-capture on risk perceptions of habituated samango monkeys

KATARZYNA NOWAK,\* SHANE A. RICHARDS, ALIZA LE ROUX, AND RUSSELL A. HILL

*Evolutionary Anthropology Research Group, Department of Anthropology, Durham University, South Road, Durham DH1 3LE, United Kingdom (KN, RAH)*

*Department of Zoology and Entomology, University of the Free State, Qwaqwa, Phuthaditjhaba 9866, South Africa (KN, ALR)*

*Department of Biological and Biomedical Sciences, Durham University, South Road, Durham DH1 3LE, United Kingdom (SAR)*

*Primate & Predator Project, Lajuma Research Centre, P.O. Box 522, Makhado 0920, South Africa (RAH)*

*Present address of SAR: CSIRO Oceans & Atmospheres, P.O. Box 1538, Hobart, Tasmania 7001, Australia*

\* Correspondent: [knowak02@gmail.com](mailto:knowak02@gmail.com)

Live-capture of animals is a widely used technique in ecological research, and previously trapped individuals often respond to traps with either attraction or avoidance. The effects of trapping on animals' risk perception are not often studied, although nonlethal effects of risk can significantly influence animals' behavior and distribution. We used a combination of experimental (giving-up densities: GUDs) and behavioral (vigilance rates) measures to gauge monkeys' perceived risk before and after a short livetrapping period aimed at ear-tagging monkeys for individual recognition as part of ongoing research. Two groups of arboreal samango monkeys, *Cercopithecus albogularis schwarzi*, showed aversion to capture in the form of generalized, group-level trap shyness after 2 individuals per group were cage trapped. We predicted that trapping would increase monkeys' antipredatory behavior in trap vicinity and raise their GUDs and vigilance rates. However, live-capture led to no perceptible changes in monkeys' use of space, vigilance, or exploitation of experimental food patches. Height above ground and experience with the experiment were the strongest predictors of monkeys' GUDs. By the end of the experiment, monkeys were depleting patches to low levels at ground and tree heights despite the trapping perturbation, whereas vigilance rates remained constant. The presence of cage traps, reintroduced in the final 10 days of the experiment, likewise had no detectable influence on monkeys' perceived risk. Our findings, consistent for both groups, are relevant for research that uses periodic live-capture to mark individuals subject to long-term study and more generally to investigations of animals' responses to human interventions.

Key words: African guenon, ear-tagging, giving-up density, livetrapping, vigilance

Live-capturing is a necessary technique in many studies of wild mammals where external markings are added to enable observers to distinguish individuals (Glander et al. 1991; Rocha et al. 2007; Stone et al. 2015), where tracking collars are affixed to study animals' movement patterns (Moehrenschrager et al. 2003), or biological samples are obtained (Fietz 2003). Seldom, however, are the effects of live-capture and associated handling on study animals' behavior explicitly investigated and even where data are available, they suggest inconsistent patterns of responses ranging from avoidance to attraction. For example, adult and juvenile coyotes (*Canis latrans*) become trap-shy after initial captures using box traps (Way et al. 2002). Coyotes that were trapped and released without sedation

strictly avoided traps in the future and, once an individual from their social group had been trapped, other group members stayed away from traps (Way et al. 2002). Trap aversion has also been reported during a related study on San Nicolas Island, where the island fox, *Urocyon littoralis dickeyi*, avoided areas in which they had been trapped, altering their ranging behavior in favor of areas where trapping had not occurred (Jolley et al. 2012). In contrast, some species become trap happy and excessive recaptures need to be reduced. For example, recaptures of the endangered fox, *U. l. clementae*, were reduced by using bait treated with odorless salt (Phillips and Winchell 2011).

Other responses to trapping include signs of short-term stress. Live-capture induces a stress response in meadow voles

(*Microtus pennsylvanicus*—Fletcher and Boonstra 2006) and ground squirrels (Delehanty and Boonstra 2009), but has no long-term effect on the stress physiology of mouse lemurs (*Microcebus murinus*), which readily habituate to trapping and are easily retrapped (Hämäläinen et al. 2014). Rhesus monkey (*Macaca mulatta*) mothers that have experienced an extended period of trapping on Cayo Santiago were more likely to maintain proximity with their infants and less likely to encourage independence of or reject infants (Berman 1989). Recent research on red colobus monkeys (*Procolobus rufomitratus*) showed that they responded similarly to darting and collaring as to a predatory attack by chimpanzees (*Pan troglodytes*—Wasserman et al. 2013)—with an acute but short-term stress response. This finding is consistent with the “risk-disturbance hypothesis,” which stipulates that human disturbance can be similar to or even exceed natural predation risk (Frid and Dill 2002). In contrast, a study of the effects of trapping on baboons (*Papio hamadryas*) and vervet monkeys (*Cercopithecus aethiops*) found no obvious effects on individual or group behavior, nor did animals become more wary of traps following previous capture (Brett et al. 1982). The length and frequency of capture, as well as the type of species under study, all appear to influence response type and magnitude.

While animals may quickly learn the association between their captors, the captors’ tools (e.g., traps), and danger, it remains unclear if nonlethal human “predators” can influence the perceived risk and foraging costs of wild animals. At the most basic level, we expect wild animals’ threat-sensitive responses to be affected by persistent human activities (Frid and Dill 2002). For example, where woolly monkeys (*Lagothrix poeppigii*) are hunted, they learn to distinguish between 3 types of humans: hunters, gatherers, and researchers, responding most strongly to hunters (Papworth et al. 2013). Other mammals, such as ungulates, may not as readily distinguish hunting from other human activities. Red deer (*Cervus elephus*) respond with increased vigilance to both recreational park users and hunters, although overall vigilance levels are higher in the hunting season (Jayakody et al. 2008). Roe deer (*Capreolus capreolus*—Benhaïem et al. 2008) and mountain gazelle (*Gazella gazelle*—Manor and Saltz 2003) become more vigilant when and where they are hunted or exposed to “human nuisance behavior.” Red deer (*Cervus elaphus*) shift habitats, trading off feeding opportunities to avoid human hunters (Lone et al. 2015), and Nubian ibex (*Capra nubiana*) do the same in response to tourists (Tadesse and Kotler 2012).

The majority of studies investigating this risk-disturbance hypothesis have assessed relatively crude changes in vigilance behavior and range use. To maintain optimal fitness, animals could make smaller-scale behavioral adjustments and discriminate between objects or contexts that vary in risk level. For example, monkeys are known to increase vigilance and decrease foraging time in the lower forest strata (Makin et al. 2012). Our study aimed to investigate short-term and local changes in microhabitat use (including vertical height) and rates of vigilance in reaction to humans and traps. We assessed if an arboreal primate, habituated to humans, will distinguish between nonthreatening

human observers, who may actually be perceived as offering protection from natural predators (Nowak et al. 2014), and potentially dangerous traps left by the observers, adjusting their behavior accordingly. We measured the effects of livetrapping, aimed at marking individuals as part of an ongoing long-term study, and subsequent placement of cage traps on monkeys’ perceived risk and associated foraging cost for 2 groups of well-habituated samango monkeys (*Cercopithecus albogularis schwarzi*). We employed 2 commonly adopted approaches for quantifying risk perceptions: giving-up densities (GUDs) and rates of vigilance. GUDs represent the amount of food a forager gives up in a food patch, with lower GUDs predicted in areas where animals feel safe and have a higher food harvest rate (Brown 1999). In contrast, higher vigilance interferes with feeding (Brown 1999; Benhaïem et al. 2008) and is expected to raise GUDs. We predicted that both indirect measures of risk (GUDs and vigilance rates) would increase relative to the baseline (pre-capture) rates, at least in the short term (days), following both live-captures and the subsequent placement of traps within the experimental area where monkeys forage on artificial feeding stations.

## MATERIALS AND METHODS

*Study site and subjects.*—We conducted our study between May and September 2013 at the Lajuma Research Centre (23°02′23″S, 29°26′05″E) in the western Soutpansberg Mountains, Limpopo Province, South Africa (Nowak et al. 2014). The site is characterized by fragments of tall moist forest (up to 20 m high) and short dry forest (up to 10 m high—Coleman and Hill 2014a). Monkeys’ natural predators include leopards (Chase Grey et al. 2013), crowned (*Stephanoaetus coronatus*) and black (*Aquila verreauxii*) eagles, caracals (*Caracal caracal*), and rock pythons (*Python sebae*). Sympatric diurnal primates are chacma baboons (*Papio ursinus*) and vervet monkeys (*Chlorocebus aethiops pygerythrus*).

We studied 2 groups of samango monkeys, which belong to the polytypic *Cercopithecus mitis* group widely distributed across Africa but rare in South Africa, where they are limited to Afromontane and coastal forest fragments (Dalton et al. 2015). They are medium-sized (up to 70 cm; 4.4 kg for adult females, 7.6 kg for adult males—Harvey et al. 1987), group-living arboreal monkeys with a mostly frugivorous diet (Coleman and Hill 2014b). Our 2 study groups consisted of 40 and 60 individuals, respectively. Since the beginning of 2012, both groups—called Barn and House—have been followed by researchers (3–4 times per week) as part of a long-term behavioral study, so are well habituated to human presence. Both groups had previously experienced GUDs experiments and cage trapping, but never in combination or in temporal proximity as in this experiment.

*Giving-up densities.*—Giving-up densities were measured for 20 days (4 consecutive days per week for 5 weeks) both before and after the pre-baiting (8 days) and live-capture periods (5 days). Artificial foraging patches were established at 16 trees, randomly selected within groups’ known winter home ranges, in short forest adjoining tall evergreen forest. At each GUDs patch, we suspended basins at 4 heights: 0.1, 2.5, 5, and 7.5 m. Each

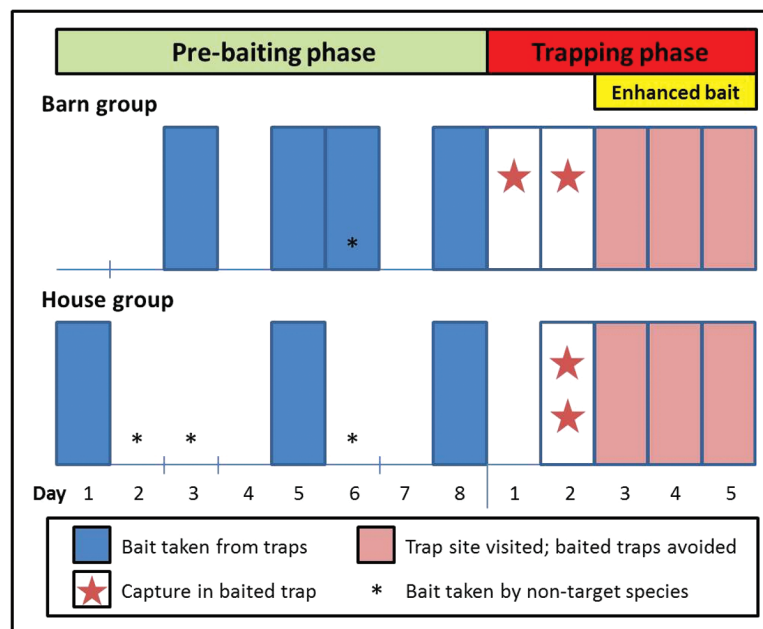
basin (46 cm in diameter) was filled with 4 liters sawdust and “baited” daily with 25 shelled raw peanut halves. We counted remaining peanuts every day after 1600h and topped up any spilled sawdust (Nowak et al. 2014). The pre-baiting and live-capture took place within this experimental patch area.

**Livetrapping.**—The main purpose of the live-capture was to ear-tag monkeys for identification purposes in the context of a large ongoing scientific research project at this site. We took advantage of these captures to answer our questions about the specificity of monkeys’ fear responses. All trapping procedures were approved by the Limpopo Province Department of Economic Development and Tourism, with ethical approval from Durham University’s Life Sciences Ethical Review Process Committee and the Anthropology Department’s Ethical Sub-Committee. Our research followed guidelines of the American Society of Mammalogists (Sikes et al. 2011).

The trapping period was preceded by 8 days of pre-baiting, consisting of baiting with orange quarters, 2 custom-made cage traps (123 cm long × 60 cm wide × 80 cm tall) per group. Monkeys (including previously ear-tagged individuals from an earlier trapping event in 2012) took oranges from traps on a regular basis during this period. Active trapping was then initiated and 4 individuals (all untagged) were trapped and marked, 2 from each group, on the first 2 days of the 5-day trapping period (Fig. 1). Samango monkeys forage as a cohesive group (Emerson and Brown 2013) and other group members were moving through the trapping area when individuals were trapped (mean neighbors within 5 m = 1.79 [ $SD = 1.89$ ]—Coleman 2013), and they dispersed in response to the capture events

and/or other individuals dispersing. Trapped individuals were hand injected with Zoletil within minutes (< 5 min) of capture by an experienced veterinarian and carried to a nearby area to be measured, ear-tagged, and finally placed in a holding cage during recovery. Three of the 4 captured individuals recovered quickly (1 adult female reacted strongly to the anesthetic), and all 4 were released within a mean of 3.7 ( $SD = 0.79$ ) hours of capture back into their social group. All animals were subsequently monitored and observed to return to typical activity patterns the following day. The traps were supplemented with additional bait, consisting of bananas and passion fruits, in the ensuing 3 days of the trapping period to try and increase the probability of further captures. These same cage traps were later replaced, open and without bait, next to GUDs trees in the final 10 days of the 20-day post-trapping experimental period.

**Vigilance.**—Vigilance behavior of monkeys while foraging on artificial food patches was recorded either by observers, standing with binoculars at no less than 20 m from GUDs trees (during monkeys’ 1st foraging bout of the day), or using camera traps (Cuddeback Attack IR; Cuddeback, De Pere, Wisconsin and Bushnell Trophy Cam; Bushnell, Overland Park, Kansas) in the absence of observers (throughout the day). “Vigilance” referred to a monkey looking or glancing up from an experimental basin to visually scan the area in an upright posture. Vigilance data were recorded from the point at which a monkey began foraging within an experimental food patch and ended when the monkey left the basin ( $n = 85$  records before trapping and 72 after trapping for Barn group; 220 before and 177 after for House group). Vigilance was extracted from camera



**Fig. 1.**—Samango monkey (*Cercopithecus albogularis schwarzi*) responses to traps placed near feeding stations during the pre-baiting and trapping phase of the study, carried out from May to September 2013 in the Western Soutpansberg Mountains, South Africa. Each day, from 6 to 18 July 2013, a trap was placed at 2 trees within the foraging range of House and Barn groups. Traps always contained food but they were not set to trigger during the pre-baiting phase. Bars depict days that samango monkeys were observed at 1 or more traps; blue bars indicate that samango monkeys removed bait from traps, whereas red bars indicate that bait within traps was avoided. On 4 days during pre-baiting baboons or vervet monkeys removed food from the traps before samango monkeys arrived (asterisk). Four samango monkeys were caught during the trapping phase (red stars): 2 adult females (AF), 1 in each group, a juvenile female (JF) in House group, and a subadult male (SM) in Barn group.

trap video footage based on the same criteria for the start and end of a bout ( $n = 16$  video clips before and 20 after capture for Barn group; 30 before and 108 after for House group) for a total of 728 records. The number of glance-ups per minute constituted “vigilance rate.” For statistical purposes, data from direct observations and camera traps were pooled following assessment that there were no statistical differences between these 2 data sources.

**Analyses.**—As prior research detected subtle effects of human followers on monkeys’ perceived risk of predation (Nowak et al. 2014), we analyzed only data from days on which monkeys were not followed from dawn to dusk by researchers. To appropriately account for the structured nature of data collection (i.e., repeated sampling at trees), and the fact that the data were highly overdispersed, we developed likelihood functions that incorporated these effects. This more general approach also allowed us to better link our biological hypotheses with our study design (Richards 2015). Specifically, we fitted discontinuous temporal models of GUDs and vigilance rates to our data to investigate whether or not our 2 experimental disturbances (live-capture and the presence of cages post-trapping) resulted in short-term changes in foraging behavior, while still allowing for any underlying gradual changes in foraging behavior. For both the GUD and the vigilance data sets, we fitted models that incorporated up to 3 predictive factors: the sampling day of the GUDs experiment (D: 1–40), the period of the study delineated by the 2 imposed disturbances (P: pre-trap [days 1–20], post-trap without trap stimulus [days 21–30], and post-trap with trap stimulus [days 31–40]), and the height of the food basin (H: ground and above-ground, which included the 3 tree-level basins). Thus, D reflects long-term responses (weeks), P reflects short-term responses (days) in the form of break points, and H reflects local responses (meters). Random variation in foraging behavior among basins, caused by unknown differences among the trees sampled, and day-to-day site-wide differences (e.g., variation in weather) also were explicitly incorporated into the models. In brief, our GUD model is a generalized example of a logistic regression, and our vigilance model is a generalized example of a nonlinear regression, where P and H are treated as discrete factors, D is a covariate, and day-to-day variation is a random effect. Also, for both models, we account for additional sources of overdispersion in the data. Full details of the statistical models can be found in [Supporting Information S1](#). Evidence that any of the 3 factors improved model parsimony and explanatory power was evaluated by performing model selection using Akaike’s Information Criterion (AIC—Richards 2015).

## RESULTS

During the 1st phase of our study (sampling days 1–20), before animals were introduced to the traps, we observed samango monkeys foraging within all of our basins. During the pre-baiting phase, when traps were placed at 2 trees within both groups’ foraging range but not set to trigger (8 consecutive days), animals continued to forage at basins placed on trees associated

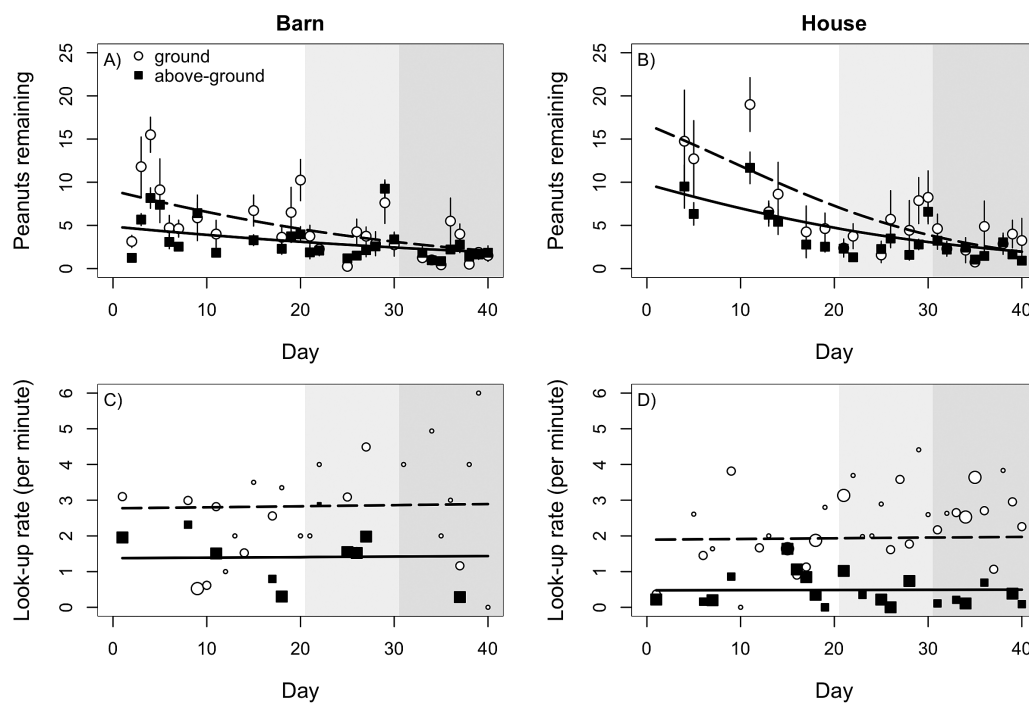
with the trap and also removed bait from the cage traps (Fig. 1). After traps were set to trigger (trapping phase) only 2 animals per group were caught and catches occurred only on the first 2 days of the trapping period (Fig. 1). No trapping location was successful on more than a single day. Animals in both groups continued to feed near the areas where the captures took place but individuals avoided approaching or entering the set traps despite the presence of significantly enhanced bait in each of the traps.

GUDs (measured as number of peanuts remaining in basins) declined gradually over the course of the study and GUDs were lower for basins placed above-ground for both groups (Figs. 2A and 2B). However, there was no obvious short-term change in GUDs after live-capture for either group (sampling days 21–40). Replacing traps back in the foraging area (days 31–40) did not raise monkeys’ perceived risk as measured by GUDs and rates of vigilance. These conclusions are supported by our AIC analyses selecting the model including height and day (H + D) as the best model for both groups (Table 1). While the model including sampling period and height (P + H) also was considered parsimonious for Barn group (Table 1), temporal changes in GUDs could be better explained by assuming a gradual decline over time rather than a response to trapping. We found no evidence of a gradual change in the rate of vigilance for either group, nor did we find any evidence of a short-term vigilance response to trapping (Figs. 2C and 2D). However, both groups significantly elevated vigilance behavior when foraging on the ground (only model H was selected for both groups; Table 1) and, in general, House group (the larger of the 2 study groups) was less vigilant.

## DISCUSSION

We found no evidence for live trapping affecting the antipredatory behavior (i.e., GUDs and vigilance rates) of these habituated samango monkeys, with the exception of observing the monkeys’ trap avoidance following initial successful captures. Their trap-shy response may represent long-term individual aversion to trapping and the trap stimulus in that no individual samangos have ever been recaptured at Lajuma (of 18 caught and tagged), while at Hogsback in the Eastern Cape, only 4 out of 64 samango monkeys were recaptured following successful capture and ear-tagging (K. Wimberger, University of Cape Town, pers. comm.). This is in contrast to mouse lemurs (Hämäläinen et al. 2014) and galagos (Charles-Dominique and Bearder 1979) which show no aversion to traps or being trapped and reenter traps on successive occasions.

Despite samango monkeys’ apparent trap aversion, we nevertheless found no further evidence that live-capture or subsequent placement of traps in the GUDs experimental area altered these samango monkeys’ perceived risk, even in the short term (neither in the days immediately following trapping nor during the 5 weeks following trapping). Monkeys’ typical antipredator behavior (e.g., vigilance and use of the ground stratum) remained unaltered after the capture events, even while the trap stimulus was present in the experimental area. Monkeys



**Fig. 2.**—Observed and predicted giving-up densities (GUDs) and vigilance rates for 2 groups of samango monkeys, *Cercopithecus albogularis schwarzi*, studied in 2013 in South Africa. Time is sectioned into 3 periods: pre-trap (days 1–20, white), post-trap without trap stimulus (days 21–30, light gray), and post-trap with trap stimulus (days 31–40, gray). Panels A and B show observed GUDs averaged across 8 trees for 2 height categories, and error bars represent 1 *SE*. Sloped lines indicate the best Akaike’s Information Criterion (AIC) model predictions, which was model D (sampling day) + H (ground or tree) for both groups. Panels C and D show the corresponding vigilance rates. Symbol size indicates the period of the observations used to calculate the mean rate: < 5 min (small), 5–15 min (medium), and > 15 min (large). Again, lines indicate the AIC-best model predictions, which was model H for both groups.

did not transfer their negative trap response (trap shyness) to our experiment, i.e., the experimental area or the artificial food sources (man-made containers/basins used in the experiment). This suggests that monkeys likely distinguish between anthropogenic sources of risk, possibly because they already had 5 weeks prior (positive and rewarding) experience with experimental food patches before the live-capture. The food patches (raw unshelled peanuts) were also of high quality and required no processing once found inside the sawdust.

Where samango monkeys face a variety of risks including conflict with people and depredation by domestic dogs, such as in Hogsback, Eastern Cape, South Africa, they will still capitalize on high-quality food in the form of fallen exotic oak acorns and seeds in people’s gardens (Wimberger et al., in press). Supplementing the cage traps in this study with additional high-quality bait (bananas and passion fruits) in the final 3 days of the live-capture, however, failed to attract the trap-averse monkeys.

Despite the absence of evidence suggesting behavioral changes in space use and vigilance in response to capture, animals did exhibit consistent, predictable variation in risk responses in relation to foraging height and experience with the GUDs experiment. Monkeys had higher GUDs at the start of the experiment, foraged less at ground level (Emerson et al. 2011; Nowak et al. 2014), and had lower vigilance rates at higher canopy levels (MacIntosh and Sicotte 2009; Campos and Fedigan 2014). The larger House group had lower vigilance rates than

the smaller Barn group, consistent with the group size effect (Hill and Cowlshaw 2002; Makin et al. 2012; Campos and Fedigan 2014). Animals also showed a steady increase in foraging proficiency over the course of the experiment, suggesting that practice and familiarity may result in falling GUDs; GUDs decreased over time at ground and tree levels, indicating monkeys’ ability to quickly adapt to their current environment and efficiently exploit newly available sources of food from which they were not easily deterred by a perturbation like live-capture.

We found no evidence of a trade-off between vigilance rates and GUDs; GUDs declined but vigilance rates were fixed throughout the duration of the study. However, we have only quantified vigilance rates and not duration of vigilance; it may be that look-up duration declined over time, which freed up time for lowering GUDs. We had enough video data of House group foraging to see if time spent at trees changed during the study, and if it differed between basin heights. We found no evidence of a day effect on the mean time spent at trees (analysis of covariance [ANCOVA];  $F_{1,31} = 2.67$ ,  $P = 0.112$ ); however, there was evidence of a height effect (ANCOVA;  $F_{1,31} = 9.40$ ,  $P = 0.004$ ) with monkeys spending less time at ground than tree canopy level (Supporting Information S2a and S2b). Over the course of the day, animals averaged shorter times at basins placed on the ground ( $3.26 \pm 0.75$  min) compared with basins placed above-ground ( $8.56 \pm 1.67$  min). These additional findings suggest that animals improved their proficiency at finding peanuts rather than spending more time at basins, given that the

**Table 1.**—Summary of the Akaike's Information Criterion (AIC) analyses of the giving-up density (GUD) and vigilance data for 2 groups of samango monkeys (*Cercopithecus albogularis schwarzi*) studied in the Western Soutpansberg Mountains, South Africa, from May to September 2013. Models incorporated up to 3 factors for both data sets: day of sampling (D), period of sampling (P), and patch height (H). *K* is the number of estimated model parameters, LL is the maximum log-likelihood, and  $\Delta$ AIC is the difference in the AIC of the model compared to the lowest AIC model. Bold  $\Delta$ AIC values indicate that the model is selected (i.e., relatively more parsimonious, given the models considered). Models were selected if they had  $\Delta$ AIC < 6 and no simpler, nested model had a lower AIC score (Richards 2008).

Model	GUD			Vigilance		
	<i>K</i>	LL	$\Delta$ AIC	<i>K</i>	LL	$\Delta$ AIC
<b>Barn group</b>						
Null	10	-1,945.1	33.7	10	-152.4	16.2
D	11	-1,940.0	25.6	11	-152.3	18.0
P	12	-1,938.9	25.2	11	-152.0	17.5
D + P	13	-1,938.9	27.2	13	-151.7	20.9
H	11	-1,933.9	13.3	11	-143.3	<b>0.0</b>
H + D	13	-1,925.2	<b>0.0</b>	12	-142.9	1.3
H + P	15	-1,924.0	<b>1.4</b>	15	-140.7	2.9
H + D + P	17	-1,923.6	4.7	16	-140.7	4.9
<b>House group</b>						
Null	10	-1,528.9	35.2	10	-285.9	51.4
D	11	-1,519.1	17.6	11	-285.8	53.2
P	12	-1,520.7	22.8	11	-285.1	51.8
D + P	13	-1,518.6	20.6	13	-284.6	54.9
H	11	-1,522.1	23.6	11	-259.2	<b>0.0</b>
H + D	13	-1,508.3	<b>0.0</b>	12	-259.1	1.8
H + P	15	-1,511.0	9.3	15	-255.6	0.8
H + D + P	17	-1,507.7	6.7	16	-255.2	1.9

amount of peanuts taken from basins increased over time but time spent at basins did not increase.

While we did not measure hormones or stress responses directly like Wasserman et al. (2013), we similarly did not find monkeys' behavior to be suggestive of a prolonged stress response as a result of our live-capture. The monkeys in our study appeared to be extremely apt at distinguishing among different forms of risk and clearly made trade-offs that optimized their exploitation of food-rich patches (Emerson and Brown 2013). While the monkeys, like coyotes and foxes (Way et al. 2002; Jolley et al. 2012), became trap-shy, their trap aversion did not result in or extend to spatial avoidance of the area in which trapping took place as it did for the carnivores. This has important implications in management terms, as the use of trapping and release would not be a worthwhile approach to deterring primates from food sources. Our research indicates that primates are unlikely to show a generalized fear response following live-capture, particularly if carried out by humans to whom they are already well habituated.

Where goals are to study primates long term by habituating them, insights about the risk-disturbance hypothesis, specifically fear, risk avoidance, and learned responses to humans and their research tools, are important for conservation managers looking to monitor endangered species. The methods we used here are generalizable to other longitudinal field studies that employ live-capture to mark and study animals. Further

comparative data are essential to gauge the relative differences among species and individuals in responses to capture and other potentially stressful research practices, such as wearing of GPS collars. This study advances our understanding of how our research and management practices may distort animal behavior—or even cause harm—and result in misinterpretation of wild animals' resilience to our presence and activities.

## ACKNOWLEDGMENTS

We thank I. Gaigher for his support and permission to work in Lajuma. Observations and experiments were carried out with ethical approval from the University of the Free State's Inter-Faculty Animal Ethics Committee and Durham University's Life Sciences Ethical Review Process Committee (KN and RAH) and approved by the Limpopo Province Department of Economic Development and Tourism. KN was funded by the Claude Leon Foundation and Durham University COFUND research fellowship program with additional support from Earthwatch. We are grateful to A. Tordiffe for his veterinary expertise during the trapping phase of this study. For assistance in the field, we thank T. Jones and Primate and Predator Project research assistants, particularly C. Scheijen. We are also grateful to B. and J. Linden and K. Wimberger for sharing knowledge about samango monkey behavior including in the context of livetrapping. We thank B. Kotler and an anonymous referee, and also editors L. Carraway and J. Merritt, for their comments that improved the final version of the manuscript. The authors have no conflicts of interest to declare.

## SUPPORTING INFORMATION

The Supporting Information document is linked to this manuscript and is available at Journal of Mammalogy online (jmmammal.oxfordjournals.org). The material consists of data provided by the author that is published to benefit the reader. The posted material is not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

**Supporting Information S1.**—Full details of statistical models and analysis of samango monkey giving-up densities and vigilance.

**Supporting Information S2a.**—ANCOVA analysis of basin visit times.

**Supporting Information S2b.**—Figure S2b.

## LITERATURE CITED

- BENHAIEM, S., ET AL. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Animal Behaviour* 76:611–618.
- BERMAN, C. 1989. Trapping activities and mother-infant relationships on Cayo Santiago: a cautionary tale. *Puerto Rico Health Sciences Journal* 8:73–78.
- BRETT, F. L., T. R. TURNER, C. J. JOLLY, AND R. G. CAUBLE. 1982. Trapping baboons and vervet monkeys from wild, free-ranging populations. *The Journal of Wildlife Management* 46:164–174.

- BROWN, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research* 1:49–71.
- CAMPOS, F. A., AND L. M. FEDIGAN. 2014. Spatial ecology of perceived predation risk and vigilance behavior in white-faced capuchins. *Behavioral Ecology* 25:477–486.
- CHARLES-DOMINIQUE, P., AND S. K. BEARDER. 1979. Field studies of lorimid behavior: methodological aspects. Pp. 567–629 in *The study of prosimian behavior* (G. A. Doyle and R. D. Martin, eds.). Academic Press, New York.
- CHASE GREY, J. N., V. T. KENT, AND R. A. HILL. 2013. Evidence of a high density population of harvested leopards in a montane environment. *PLoS One* 8:e82832.
- COLEMAN, B. T. 2013. Spatial and temporal determinants of samango monkey (*Cercopithecus mitis erythrarchus*) resource acquisition and predation avoidance behaviour. Ph.D. dissertation, Durham University, Durham, United Kingdom.
- COLEMAN, B. T., AND R. A. HILL. 2014a. Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour* 88:165–173.
- COLEMAN, B. T., AND R. A. HILL. 2014b. Biogeographic variation in the diet and behaviour of *Cercopithecus mitis*. *Folia Primatologica* 85:319–334.
- DALTON, D. L., ET AL. 2015. New insights into samango monkey speciation in South Africa. *PLoS One* 10:e0117003.
- DELEHANTY, B., AND R. BOONSTRA. 2009. Impact of live trapping on stress profiles of Richardson's ground squirrel (*Spermophilus richardsonii*). *General and Comparative Endocrinology* 160:176–182.
- EMERSON, S. E., AND J. S. BROWN. 2013. Identifying preferred habitats of samango monkeys (*Cercopithecus (nictitans) mitis erythrarchus*) through patch use. *Behavioural Processes* 100:214–221.
- EMERSON, S. E., J. S. BROWN, AND J. D. LINDEN. 2011. Identifying Sykes' monkeys', *Cercopithecus albogularis erythrarchus*, axes of fear through patch use. *Animal Behaviour* 81:455–462.
- FIEZ, J. 2003. Pair living and mating strategies in the fat-tailed dwarf lemur (*Cheirogaleus medius*). Pp. 214–231 in *Monogamy: mating strategies and partnerships in birds, humans and other mammals* (U. H. Reichard and C. Boesch, eds.). Cambridge University Press, Cambridge, United Kingdom.
- FLETCHER, Q. E., AND R. BOONSTRA. 2006. Impact of live trapping on the stress response of the meadow vole (*Microtus pennsylvanicus*). *Journal of Zoology (London)* 270:473–478.
- FRID, A., AND L. DILL. 2002. Human-caused disturbance stimuli as a form of predation risk. *Ecology and Society* 6:11.
- GLANDER, K. E., L. FEDIGAN, L. FEDIGAN, AND C. A. CHAPMAN. 1991. Field methods for capture and measurement of three monkey species in Costa Rica. *Folia Primatologica* 57:70–82.
- HÄMÄLÄINEN, A., M. HEISTERMANN, Z. S. E. FENOSOA, AND C. KRAUS. 2014. Evaluating capture stress in wild gray mouse lemurs via repeated fecal sampling: method validation and the influence of prior experience and handling protocols on stress responses. *General and Comparative Endocrinology* 195:68–79.
- HARVEY, P. H., R. D. MARTIN, AND T. H. CLUTTON-BROCK. 1987. Life histories in comparative perspective. Pp. 181–196 in *Primate societies* (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, eds.). Cambridge University Press, Cambridge, United Kingdom.
- HILL, R. A., AND G. COWLISHAW. 2002. Foraging female baboons exhibit similar patterns of antipredator vigilance across two populations. Pp. 187–204 in *Eat or be eaten: predator sensitive foraging among primates* (L. E. Miller, ed.). Cambridge University Press, Cambridge, United Kingdom.
- JAYAKODY, S., A. M. SIBBALD, I. J. GORDON, AND X. LAMBIN. 2008. Red deer *Cervus elephus* vigilance behaviour differs with habitat and type of human disturbance. *Wildlife Biology* 14:81–91.
- JOLLEY, W. J., ET AL. 2012. Reducing the impacts of leg hold trapping on critically endangered foxes by modified traps and conditioned trap aversion on San Nicolas Island, California, USA. *Conservation Evidence* 9:43–49.
- LONE, K., L. E. LOE, E. L. MEISINGSET, I. STAMNES, AND A. MYSTERUD. 2015. An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Animal Behaviour* 102:127–138.
- MACINTOSH, A. J. J., AND P. SICOTTE. 2009. Vigilance in ursine black and white colobus monkeys (*Colobus vellerosus*): an examination of the effects of conspecific threat and predation. *American Journal of Primatology* 71:919–927.
- MAKIN, D. F., H. F. P. PAYNE, G. I. H. KERLEY, AND A. M. SHRADER. 2012. Foraging in a 3-D world: how does predation risk affect space use of vervet monkeys? *Journal of Mammalogy* 93:422–428.
- MANOR, R., AND D. SALTZ. 2003. Impact of human nuisance disturbance on vigilance and group size of a social ungulate. *Ecological Applications* 13:1830–1834.
- MOEHRENSCHLAGER, A., D. W. MACDONALD, AND C. MOEHRENSCHLAGER. 2003. Reducing capture-related injuries and radio-collaring effects on swift foxes. Pp. 107–113 in *The swift fox: ecology and conservation of swift foxes in a changing world* (L. Carbyn and M. A. Sovada, eds.). University of Regina Press, Regina, Saskatchewan, Canada.
- NOWAK, K., A. LE ROUX, S. A. RICHARDS, C. P. J. SCHELIEN, AND R. A. HILL. 2014. Human observers impact habituated samango monkeys' perceived landscape of fear. *Behavioral Ecology* 25:1199–1204.
- PAPWORTH, S., E. J. MILNER-GULLAND, AND K. SLOCOMBE. 2013. Hunted woolly monkeys (*Lagothrix poeppigii*) show threat-sensitive responses to human presence. *PLoS One* 8:e62000.
- PHILLIPS, R. B., AND C. S. WINCHELL. 2011. Reducing nontarget recaptures of an endangered predator using conditioned aversion and reward removal. *Journal of Applied Ecology* 48:1501–1507.
- RICHARDS, S. A. 2008. Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology* 45:218–227.
- RICHARDS, S. A. 2015. Likelihood and model selection. Pp. 58–80 in *Ecological statistics: contemporary theory and application* (G. Fox, S. Negrete-Yankelevich, and V. Sosa, eds.). Oxford University Press, Oxford, United Kingdom.
- ROCHA, V. J., ET AL. 2007. Techniques and trap models for capturing wild tufted capuchins. *International Journal of Primatology* 28:231–243.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- STONE, A., P. H. CASTRO, F. MONTEIRO, L. RUIVO, AND J. SILVA, Jr. 2015. A novel method for capturing and monitoring a small neotropical primate, the squirrel monkey (*Saimiri collinsi*). *American Journal of Primatology* 77:239–245.
- TADESSE, S. A., AND B. P. KOTLER. 2012. Impact of tourism on Nubian ibex (*Capra nubiana*) revealed through assessment of behavioral indicators. *Behavioral Ecology* 23:1257–1262.
- WASSERMAN, M. D., C. A. CHAPMAN, K. MILTON, T. L. GOLDBERG, AND T. E. ZIEGLER. 2013. Physiological and behavioral effects of capture darting on red colobus monkeys (*Procolobus rufomitratus*)

with a comparison to chimpanzee (*Pan troglodytes*) predation. *International Journal of Primatology* 34:1020–1031.

WAY, J. G., I. M. ORTEGA, P. J. AUGER, AND E. G. STRAUSS. 2002. Box-trapping eastern coyotes in southeastern Massachusetts. *Wildlife Society Bulletin* 30:695–702.

WIMBERGER, K., K. NOWAK, AND R. A. HILL. In press. Reliance on exotic plants by two groups of endangered samango monkeys,

*Cercopithecus albogularis labiatus*, at their southern range limit. *International Journal of Primatology*.

*Submitted 1 January 2016. Accepted 11 April 2016.*

*Associate Editor was Leslie N. Carraway.*