TITLE: Water availability impacts habitat use by red-fronted lemurs (*Eulemur rufifrons*): an experimental and observational study

RUNNING TITLE: Water availability impacts wild lemur ranging

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ACKNOWLEDGEMENTS

We would like to thank Léonard Razafimanantsoa and the field assistants and staff of the German Primate Center (DPZ) Research Station at Kirindy Forest and the CNFEREF Morondava for supporting our study. We appreciate Mael Jaonasy Frangico's valuable assistance with the data collection for this project. We thank James Herrera for feedback on the analytical methods, and three anonymous reviewers, Dr. Onja Razafindratsima, and Prof. Joanna Setchel for feedback on the manuscript. We also would like to thank MICET (Madagascar Institute for the Conservation of Tropical Environments) for their support and facilitation of permits. This study was funded by NSF-1613482, the Margot Marsh Biodiversity Foundation, Primate Conservation, Inc., and Duke Graduate School International Dissertation Travel Grant.

TITLE: Water availability impacts habitat use by red-fronted lemurs (*Eulemur rufifrons*): an experimental and observational study

ABSTRACT: With the predicted increase in extreme weather events as a result of global climate change, animals living in dry or seasonally dry habitats are likely to experience dramatic fluctuations in water availability from season to season and year to year. Understanding how animals respond to short-term changes in water availability is paramount for future conservation and management of water-dependent wild populations. We investigated how short-term changes to the availability of water influenced habitat use of four groups of red-fronted lemurs (*Eulemur rufifrons*) in a dry deciduous forest in western Madagascar using detailed spatial data collected from GPS collars over 15 weeks. We experimentally manipulated water availability in the habitat, and compared ranging patterns of the lemurs during the experiments to those before and after the experiments. Lemur groups shifted the intensity of their habitat use relative to changes in natural and experimental water availability. Specifically, lemurs were more likely to spend time in areas near experimental water sources during the experiment than in the same areas without water. Lemurs were less likely to spend time near previous habitual water sources when experimental water sources were available. We observed shifts in ranging intensity in response to natural changes to water availability when waterholes disappeared across the dry season. Our findings support the importance of water for shaping wild animal ranging patterns. We propose that water should be a primary consideration in future studies of habitat use, especially given the potential for climate change and human land use to further alter water availability for wild animals.

KEYWORDS: *Eulemur rufifrons*, GPS collars, habitat use, ranging, water scarcity

INTRODUCTION

Given the increasing threat of extreme weather events predicted with future climate change (Schlaepfer et al. 2017; Trenberth et al. 2014; Wanders and Wada 2015), understanding the flexibility of animals to respond to changes in water availability will be essential for future conservation and management decisions of wild populations in dry environments. Indeed, in arid or seasonally dry habitats, water may be among the most important determinants of movement and habitat use for some species (Bleich et al. 2010; Boroski and Mossman 1996; Marshal et al. 2006). Ecologists have dedicated considerable effort to understand how the distribution of food resources determines animals' habitat use (Davies et al., 2013; Kelley, 2013; Kittle, Bukombe, Sinclair, Mduma, & Fryxell, 2015; Seidel & Boyce, 2015; van Gils et al., 2015). However, less is known about how individual animals' habitat use responds to short-term changes in water availability, such as drying of ephemeral water sources across the course of a dry season or drought (Amorim et al. 2018). Many animal populations have suffered high mortality during droughts (Alberts 2018; Altmann et al. 1985; Foley et al. 2008; Gordon et al. 1988; Hamilton 1985; Knight 1995; Sapolsky 1986), highlighting the potential strength of selection on adaptations for acquiring water and responding flexibly to changes in water distribution in dry habitats.

In primates, several studies provided observational evidence that ranging patterns respond to the availability of water sources. For example, several species are attracted to areas of the habitat that contain water sources, including olive baboons (*Papio anubis*) (Barton et al. 1992), red-fronted lemurs (*Eulemur rufifrons*) (Scholz and Kappeler 2004), white-faced capuchins (*Cebus capucinus*) (Campos and Fedigan 2009), and chacma baboons (*Papio ursinus*) (Noser and Byrne 2007, 2014). A study of black howler monkeys (*Alouatta pigra*) found that heat stress and water availability in food influence drinking behavior (Dias et al. 2014). However, some primate species are rarely observed to drink water outside of the water acquired through their foods, even in dry habitats. For example, in Madagascar's dry deciduous forests, red-fronted lemurs frequently drink from external water sources, but sympatric Verreaux's sifakas (*Propithecus verreauxi*) do not (pers. obs.). Patterns of water consumption, and thus the relative impact of water on ranging behavior, are likely to vary across species and depend on environmental factors like the water content of food items and rainfall.

Previous investigations of the impacts of water on habitat use by wild primates have primarily been observational in design, leaving open the possibility that water may co-occur with other valuable resources rather than causatively driving ranging patterns on a short timescale. Supporting this possibility, even desert-adapted small mammals that do not drink water increase their use of areas near introduced water sources because they are richer in foods like insects or succulent plants (Switalski and Bateman 2017). Similarly, some bats forage above water pools in addition to drinking from them (Korine et al. 2015). These examples highlight that in the absence of field experiments, the apparent influence of water on habitat use could be misattributed to the overlapping distribution of other resources, such as food, sleeping sites, or territory boundaries, rather than water alone. The location of water is expected to drive habitat use for certain dry-habitat living primates. However, controlled experiments that test hypotheses concerning the role of water in determining wild primate ranging patterns are lacking, despite the success of similar experiments on feeding behavior in contributing to our understanding of primate ranging (Janson & Di Bitetti, 1997; Janson, 2014).

Here, we took a combined experimental and observational approach to test the hypothesis that the spatiotemporal availability of water resources determines patterns of habitat use in wild red-fronted lemurs in western Madagascar. Red-fronted lemur groups in the dry deciduous forests in this region drink from waterholes regularly, and previous observational work demonstrated that non-resident groups make long trips to reach water sources within the study site (Scholz and Kappeler 2004). It is unknown whether this species can survive on water from its diet alone, but observations suggest that red-fronted lemurs require drinking water in this habitat based on the frequency with which they drink from waterholes. We collected spatial data with GPS collars to quantify lemur habitat use patterns and estimate utilization densities relative to the locations of naturally occurring water sources. Following a five-week observation period, we also introduced artificial water sources into the lemurs' home ranges for five weeks, and subsequently removed the water sources for an additional five-week period.

We tested three sets of predictions of the hypothesis that the availability of water influences habitat use in red-fronted lemurs. First, compared to patterns of habitat use before the artificial waterhole experiment, we predicted that lemurs would spend more time in areas of the habitat close to introduced water sources during the experiment. As a corollary to this prediction, we also predicted that the lemurs would spend less time close to naturally occurring water sources during the experiment than before. Second, after the experiment ended, we expected these patterns to reverse, with lemurs ranging more intensively near natural waterholes and less so near artificial waterholes after the experiment. Finally, we predicted that changes in natural water availability would be reflected in the lemurs' habitat use. Focusing specifically on one of the remaining waterholes at the end of the dry season, we predicted lemur groups to use the area surrounding this waterhole more as other sources of water disappeared over the course of the dry season.

METHODS

Study System

We studied a wild, habituated population of red-fronted lemurs living in Kirindy Forest, a dry deciduous forest in western Madagascar. Kirindy Forest/Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie (CNFEREF) is a protected forestry reserve located at 44°39' E 20°03' S, and the red-fronted lemurs at this site have been studied for more than 20 years (Kappeler and Fichtel 2012). Rainfall is extremely low, typically <40 mm of rain during the entire local dry season (May-October), when the river that flows through the study site dries up until only several small standing waterholes remain in the riverbed in the late dry season (Kappeler and Fichtel 2015; Scholz and Kappeler 2004). Waterholes ranged in size from <0.5m to >80m at their longest diameter, and decreased continuously in size across the course of the dry season. Many waterholes dry up completely before the end of the dry season, though several of the larger waterholes typically last for the duration of the dry season. Red-fronted lemurs and other mammal and bird species regularly frequent these waterholes and seem to depend upon them as a water source throughout the dry season.

Ethical Note

The protocol for this research was approved by Duke University's Institutional Animal Care and Use Committee (Protocol A008-17-01) and the Malagasy Ministry of the Environment, Water, and Forests (145/16/MEEF/SG/DGF/DSAP/SCB.Re).

Experimental Procedure

To monitor the lemurs' habitat use, we affixed GPS collars (Collar 1AA, 55g, 1600mAh, e-obs GmbH, Gruenwald, Germany) to one adult male from each of four resident groups while he was incapacitated from routine tranquilizer darting (Koch et al. 2016; Pyritz et al. 2011; Springer et al. 2015). These groups' ranges overlap substantially and are close to the river year-round (groups B, F, J, and Q). At the time of study, these groups comprised 7, 4, 10, and 3 individuals respectively, and individuals could be identified by differently colored and tagged collars. The GPS devices were programmed to record one GPS point every hour for a total of 24 fixes per day. The devices attempted to connect to satellites for two minutes, and if unsuccessful, would re-initiate the following hour. We collected data on the lemur groups' geographic positions for 15 weeks during the dry season (July 5-October 18, 2017) and downloaded the data remotely from the collars using a basestation device (e-obs BaseStation II). One group (J) was collared with the GPS device two weeks later than the other groups due to logistical challenges of darting. Red-fronted lemur groups are cohesive, and the movements of one individual are likely representative of the entire group (Pyritz et al. 2011, 2013).

We observed each lemur group for 2-3 days per week between the hours of 07:00-11:00 and 13:00-17:00, and recorded their use of any water source. For another study, we monitored the natural waterholes with motion-activated video camera traps (Bushnell 119875C Trophy Cam). We used these records combined with direct observation to approximate the natural waterhole that each group used most habitually, although the groups would occasionally use different natural waterholes.

Following a five-week baseline observation period (three weeks for Group J), we conducted a five-week experiment in which an artificial waterhole was installed for each group at a location that the group was known to frequent regularly, based on observations during the dry season of the previous year and suggestions from experienced Malagasy field assistants. We selected locations that groups used commonly and within their typical home ranges in part to increase the probability that the lemur groups would find and use the artificial waterholes, but also to minimize any energetic costs that lemurs might incur as a consequence of the experiment or their future use of these areas as a result of their memory of the experiment. Each artificial waterhole consisted of two 10-L black rubber buckets (livestock feed buckets) placed in shallow holes dug into the ground in an area of the habitat judged to be hidden from forest trails and covered from aerial predators (Fig. 1). Two motion activated video cameras (same as used at the natural waterholes, see above) were positioned in the area surrounding the artificial waterhole to monitor lemurs' use of the artificial waterholes. We filled in soil around the edges of the bucket so that the top edge of the bucket was even with the surrounding earth. For the first three weeks of the experiment, we transferred water to the buckets from one natural waterhole; in the final two weeks, we manipulated the quality of the water for another experiment not discussed here (Amoroso et al. 2019). Water of the same quality as or cleaner than the naturally available water was present in at least one of the buckets at all times for the duration of the five weeks. We added water (10 L) to each bucket until it was full, to make the water level even with the earth. We topped off the water every 2-3 days and dumped, scrubbed with dish soap, rinsed, and refilled the buckets with new water once per week.

Figure 1. TOP: Artificial waterhole experimental setup in Kirindy Forest, Madagascar. Two 10-l buckets inserted into holes in the ground and filled with water to manipulate the distribution of water in the habitat. **BOTTOM: Two red-fronted lemurs (*Eulemur rufifrons*) next to and drinking from an artificial waterhole.** Video camera trap shown in background. Photos taken September 2017.

We added water to the artificial waterholes on 23 July 2017. After one week, the cameras had not recorded any instances of red-fronted lemurs investigating the artificial waterholes. To be sure that the lemurs were aware of the water we had added to their habitat, we took advantage of previous research in this population that trained the lemurs to approach a clicker (e.g. as used in dog training) for experiments and routine weighing (Schnoell and Fichtel 2012). We used this clicker noise during the second week after the artificial waterhole installation to opportunistically attract each group to the artificial waterhole when they were located nearby (within 100 m of the artificial waterhole). We did this twice per group during the second week after the artificial waterhole installation. Upon observing the lemurs' apparent neophobia toward the artificial waterholes at their initial approach, we attempted to make the artificial waterholes appear more similar to the natural waterholes by adding a handful of soil and leaves from the surrounding area to the buckets; following this adjustment, the lemurs drank from the artificial waterholes. After the second use of the clicker, at least one individual from every group drank from the artificial waterhole, which we judged to indicate that the lemurs would be aware of the new water source without any further intervention. At subsequent visits, all individuals of the focal groups drank from the artificial waterholes.

For the statistical analysis, we marked the beginning of the experimental period after the end of the clicker use, once all lemur groups located and drank from their artificial waterholes independently. We expected that the clicker would not have large impacts on our measurements, given the short distance and time period over which we affected the lemurs' movement. However, if using the clicker on two occasions per group detectably influenced the range estimates of the lemur groups, this would have occurred before the start of the experimental period. Thus, if the use of the clickers introduced any bias into the analysis, we expected it to bias the results in the opposite direction of our predictions, by increasing the time lemurs spent near the artificial waterholes before we marked the start of the experiment.

During the experimental period we continued to follow the lemur groups and monitor their use of artificial waterholes with the motion-activated video camera traps, specifically noting the dates and times when lemurs were observed drinking from the artificial waterholes. The experimental period lasted for five weeks, and was complete when the water remaining in the artificial waterholes dried up after we stopped replenishing them. We continued to monitor the lemur groups via GPS collars for five more weeks after the experiment ended.

Analyses

We quantified the probabilities of lemur groups inhabiting areas of the forest using a dynamic Brownian bridge movement model (dBBMM) (function *brownian.bridge.dyn* in package “move” v.3.0.2 in R v.3.5.1) (Horne et al. 2007; Kranstauber et al. 2012; R Development Core Team 2011). A dBBMM estimates the probability that a moving object is located in an area based on known points (in this case, points from the GPS collars) taken in sequence over relatively short time intervals, assuming a conditional random walk, or Brownian motion between consecutive points (Horne et al. 2007; Sawyer et al. 2009). The model estimates a probability density connecting each pair of successive points that incorporates the location error and the time elapsed between points. Thus, it estimates a larger area of probability around points with higher error estimates or between points with a longer time interval, and accounts for the temporal autocorrelation in the data. In this study, the location error of each GPS fix was estimated by the GPS device itself. In addition, the dBBMM dynamically estimates the

Brownian motion variance, a measure of diffusiveness in the animal's path, based on a user-defined sliding "window" and "margin," two specified numbers of time steps that define how the variance from a direct path is measured (Kranstauber et al. 2012). After plotting the raw movement paths and visually examining the data, we judged that setting the "window" to 13 time steps (i.e. approximately two windows per day) and "margin" to 3 was sufficient to identify relevant changes in movement behavior. Using all successive points in each individual's trajectory, we thus estimated the probability of occupancy for each group in the habitat.

To determine how probability of occupancy changed across experimental conditions, we created dBBMMs to compare habitat use before and during the experiment, and during and after the experiment, respectively. The paired dBBMMs were determined on the same geographic grid, so that probability estimates were directly comparable across conditions. A 70-m grid was drawn for each group that included a 300-500 m buffer around the group's extent (depending on the size of the range, per requirements of the *brownian.bridge.dyn* function). Then, for each analysis, a subset of those grid squares within 600 m of the artificial waterhole of interest for the group was selected. This process maximized the sample size of estimated probabilities without exceeding the minimum true sample size of GPS points collected for any group during a single period of the study, and eliminated the large number of grid cells with zero probability from the buffers around the extent of the range. We subtracted the probability distribution of the earlier time period from that of the later time period to create a distribution of the change in probability from one time period to the next. We calculated the distance from each location in this distribution (the center of each grid cell) to the artificial waterhole for that group. We repeated this analysis to compare habitat use before and during the artificial waterhole experiment and to compare during and after the experiment for each lemur group.

Our approach of subtracting the two probability distributions from one another allowed for straightforward interpretation. If the lemurs used a particular area consistently before, during, and after the experiment, the probability of occupying the relevant grid square would not change across these timepoints. Our method thus detected changes in intensity of use in either direction from one timepoint to the next. In this analysis, we assumed that increases in probability in the areas closest to the artificial waterholes during the experiment were a consequence of the new water availability in this area. We also expected the lemurs to change their ranging intensity in other areas of the forest: not only reduced ranging in areas near natural waterholes in response to our experiment, but also in response to unrelated changes in their surroundings, such as in food availability and inter-group dynamics.

We used a model-fitting approach to determine how the distance from an area of the habitat to a water source influenced the change in intensity of ranging before, during, and after the experiment in this area. We compared the AIC scores of an exponential model to a null (intercept-only) model to determine which model the data supported (using the gnls function of the "nlme" package in R; Pinheiro et al., 2018). An exponential model was chosen to compare to the null because its shape corresponded to our expectation that the greatest increases in habitat use during the experiment would take place closest to the artificial waterholes, and fewer changes would occur at distances farther from the artificial waterholes.

To control for spatial autocorrelation, we fitted each null model with several spatial correlation structures, and applied the one that produced the lowest AIC score to both the null and exponential models for each group-timepoint comparison (corStruct argument in the gnls function, see Tables S1 and S2 for details). A model was considered more favorable than the alternative if it had a ΔAIC > 2. Thus, if an exponential model were better supported by the data than the null – i.e., if it had a lower AIC score by more than two units – we interpreted this finding to indicate that the presence or absence of a water source in a particular area of habitat increased or decreased the lemurs' probability of using that area, respectively.

In addition to the analysis of the probability of occupancy within the whole ranging area relative to the distance from the artificial water source, we selected a subset of the grid cells that we predicted to be especially sensitive to changes in water availability: those cells within a 140m buffer (two grid cells' distance) of a line drawn directly between a group's artificial waterhole and a natural waterhole that they were observed to use. We expected to see the strongest relationship (i.e. with less noise) between the distance from the group's artificial waterhole and change in probability of occupancy along this line. We used generalized least square regressions of these points from all groups combined (to increase sample size) to compare the fit of the maximum likelihood linear model that included distance to a null (intercept-only) model (using the lme function of the nlme package in R; Pinheiro et al., 2018). We controlled for group by including it as a random effect in both models and for spatial autocorrelation by adding a spatial correlation term to both models, following the procedure described above.

Finally, we investigated changes in natural waterhole use as the dry season progressed. At the end of the dry season, water only remained in one small area of the riverbed (in several natural waterholes, including one that we identify as NWH17), and the natural waterholes used previously by three groups (B, F, and J) had dried up. If water availability has a major impact on lemurs' habitat use, we expected that probability of occupancy would be higher in locations closer to NWH17 in the late dry season, as compared to earlier in the dry season (i.e., before and after the experimental manipulation). For these three groups, we repeated the analysis of the change in probability along the line between the natural waterhole used before the experiment and NWH17, following the same procedure described above for the three groups combined. Group Q was not included in this analysis because a natural waterhole that they typically used before the experiment was still available after the experiment, so we expected little change in the probability of this group's occupancy near this natural waterhole.

RESULTS

Across the 15-week period, the GPS devices collected a total of 9474 points, or a mean of 2496 points per device (SD: +/- 241.7). The mean location error estimated by the devices was 15.99m (SD: +/- 12.74m). Lemur groups took approximately two weeks (15.25 +/- 1.7 days) to begin using the artificial waterholes on their own after the initial addition of water. After the start of the experimental period, lemur groups visited and drank from the waterholes once per day (mean = 23.19 +/- 19.8h), excluding activations of the camera or observations within an hour of each other, which we considered part of the same visit. All individual members of each group drank from the artificial waterholes.

Plots of utilization densities for the groups before, during, and after the experiment revealed an apparent change in habitat use intensity during the experiment, although these changes are more marked in some groups than others (Fig. 2). Two types of changes were visible: changes to the boundaries of the utilization densities and to the intensity of use within the previous boundaries. The pre- and post-experiment plots also demonstrated how natural fluctuations in water availability influence ranging, causing groups to increase intensity of use in new areas of the forest where the only waterholes remained by the end of the study period.

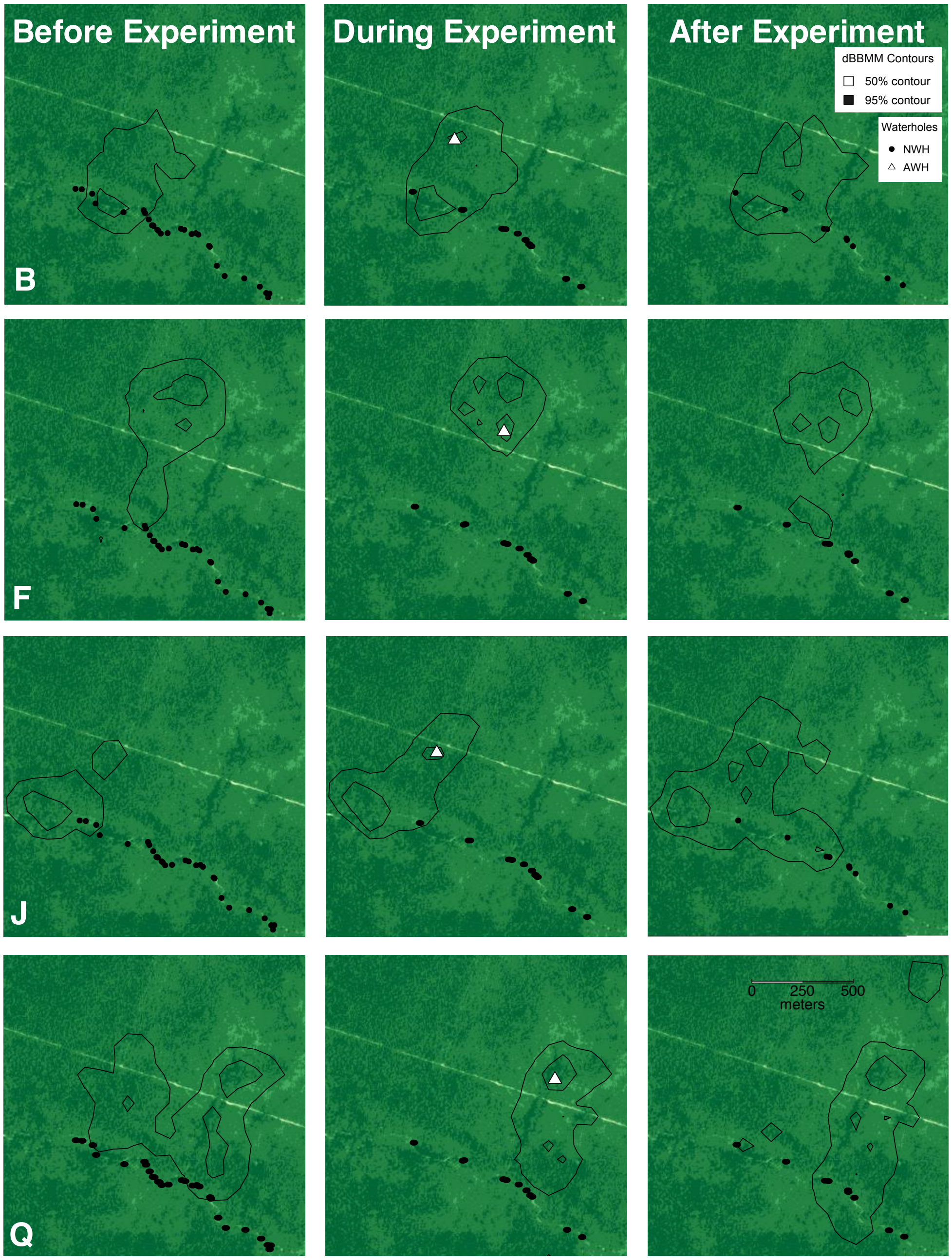

Figure 2. Utilization densities based on a dynamic Brownian bridge movement model for each red-fronted lemur (*Eulemur rufifrons*) group at three experimental time periods and locations of natural waterholes (NWHs) and artificial waterholes (AWHs) in Kirindy Forest, Madagascar. Each time period was 5 weeks in duration during a study period spanning July-October 2017. The lighter shaded polygon indicates the 95% utilization density range, and the darker shaded polygon represents the 50% utilization density range. Black circular points represent the NWHs present at the start of each period; points that are present in earlier plots but absent from

later ones indicate NWHs that dried from one period to the next. White triangular points represent the AWH for the group that is plotted.

When assessing change in ranging patterns as a function of distance from the artificial waterhole, we found that the exponential model offered a better fit to the data for all four groups in the comparison of ranging patterns before and during the experiment, and for three of four groups in the comparison of ranging patterns during and after the experiment (Table 1). These results are consistent with changes in habitat use toward the artificial waterhole, as predicted.

Table 1: AIC scores for exponential and null models of the change in probability of red-fronted lemur (*Eulemur rufifrons*) occupancy in grid cells relative to the location of an artificial waterhole during an experiment that manipulated water distribution in Kirindy Forest, Madagascar in July-October 2017. Support for the exponential model over the null model indicates that the locations closest to the artificial waterhole underwent the most significant changes in the probability of occupancy, and in the predicted direction. Shaded cells indicate which model had the lower AIC score, or is more likely given the data. Absolute values of the difference in AIC scores between the two models are provided in the rightmost column, which had to be >2 to support one model over the other.

Group	Time Period	AIC Exponential	AIC Null	ΔAIC
B	During-Before Experiment	-2454	-2435	19
	After-During Experiment	-2596	-2449	147
F	During-Before Experiment	-2913	-2887	26
	After-During Experiment	-2536	-2540	4
J	During-Before Experiment	-2275	-2256	19
	After-During Experiment	-1680	-1642	38
Q	During-Before Experiment	-3062	-2938	124
	After-During Experiment	-3047	-2976	71

When comparing models of the change in occupancy after compared to during the experiment for Group F, the data support the null model better than the exponential model. For all groups, the grid squares closest to the artificial waterhole were used more during the experiment relative to periods before and after the experiment (Figs. 3 and 4). Areas at various distances from the artificial waterhole also underwent changes in the intensity of use. These changes may be stochastic, or due to ecological factors that were not this study's focus, such as natural changes in food availability, interactions with other groups, or movements of predators. Note, our dataset measured a change in probability, or the difference between two sets of probability values. We calculated these probabilities for over 100 grid squares (over 300 for some analyses), and the probabilities sum to 1, which explains the small values on the y-axes in the plots corresponding to these and subsequent results. For context, if the lemurs used all of 100 grid squares equally, the probability of their occupancy in each square would be 0.01; thus, an increase of 0.05 in one square would indicate a 5% increase in probability of use in that grid cell. While this is apparently a small increase in use in that one cell, when these changes are summed across multiple nearby grid cells, they can account for substantial differences in habitat use.

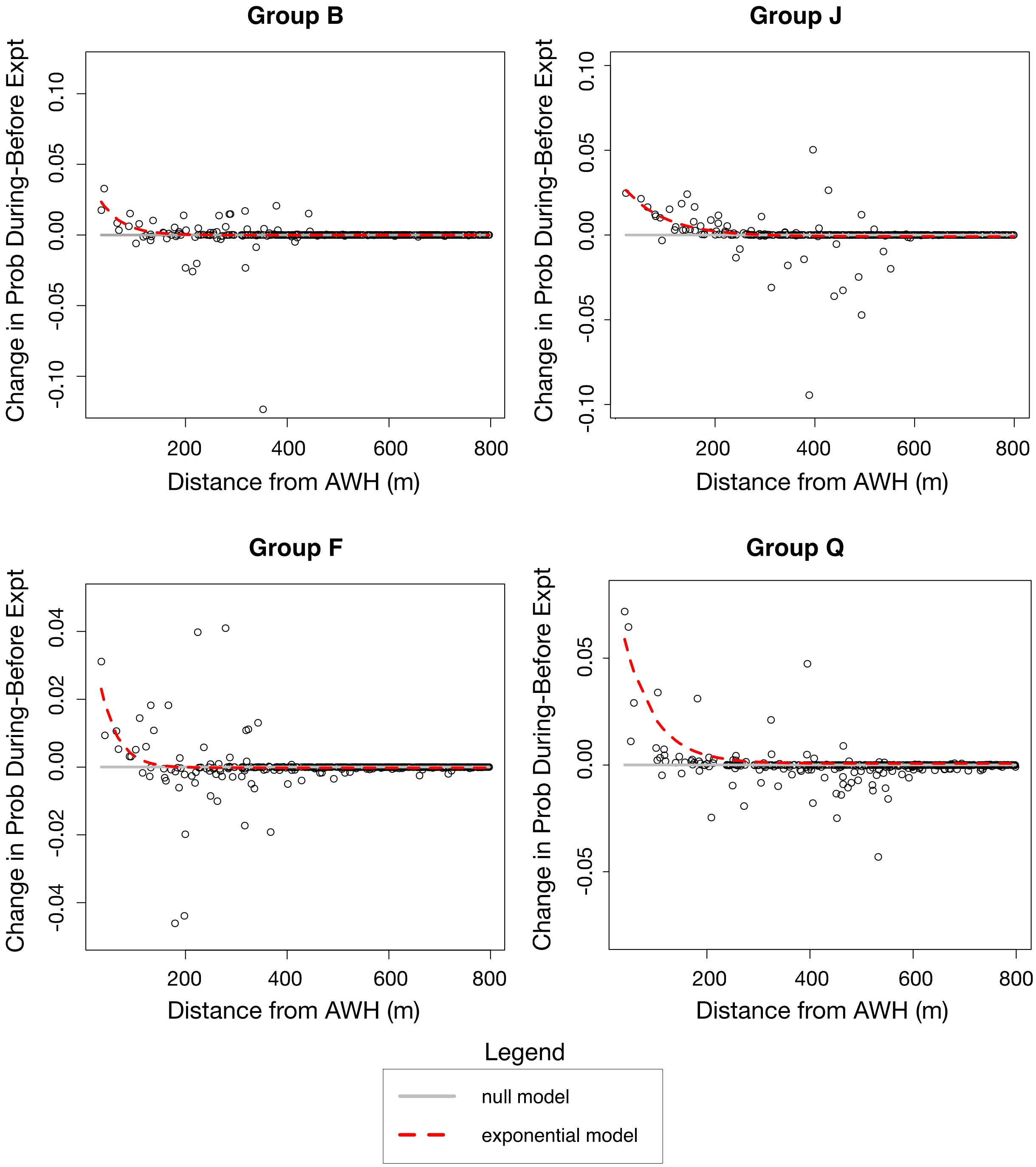
Group B
Group J
Group F
Group Q
Change in Prob During-Before Expt
Distance from AWH (m)
0.10
0.05
0.00
-0.05
-0.10
0.04
0.02
-0.02
-0.04
200
400
600
800
Legend
null model
exponential model

Figure 3. Comparison of exponential and null models of the relationship between change in probability of occupancy and distance from an artificial waterhole (AWH) before and during an experiment for four red-fronted lemur (*Eulemur rufifrons*) groups. The experiment manipulated the distribution of water in Kirindy Forest, Madagascar in July-October 2017. Each point represents the change in probability at a given grid square of the group's range; positive probabilities indicate an increase in occupancy during the experiment relative to before, and negative probabilities indicate a decrease during relative to before. The gray solid line indicates the fitted line for the null model, and the red dotted line indicates the fitted line for the exponential model.

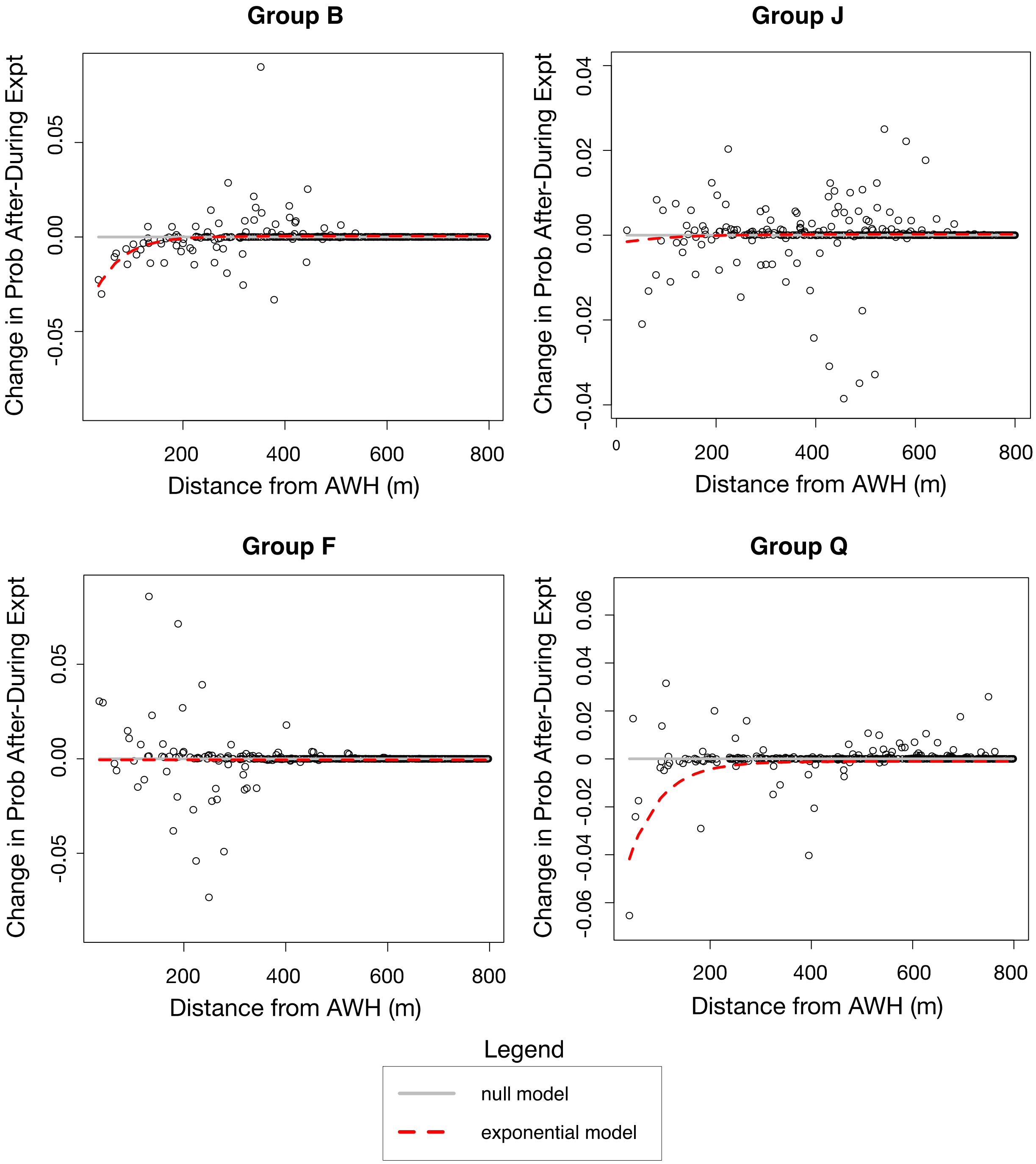

Figure 4. Comparison of exponential and null models of the relationship between change in probability of

occupancy and distance from the artificial waterhole (AWH) during and after the experiment for four red-fronted lemur (*Eulemur rufifrons*) groups. The experiment manipulated the distribution of water in Kirindy Forest, Madagascar in July-October 2017. Each point represents the change in probability at a given grid square of the group's range. The gray solid line indicates the fitted line for the null model, and the red dotted line indicates the fitted line for the exponential model.

When we analyzed only the points along the line between a group's artificial waterhole and its habitually used natural waterhole before the experiment, we found that distance was a statistically significant, although relatively small negative predictor of change in probability of occupancy (distance coefficient=-0.000036, *P*<0.01, t=-3.48, DF=143; Fig. 5, Table S1). The data supported a linear model that included distance better than the null model (Table 2).

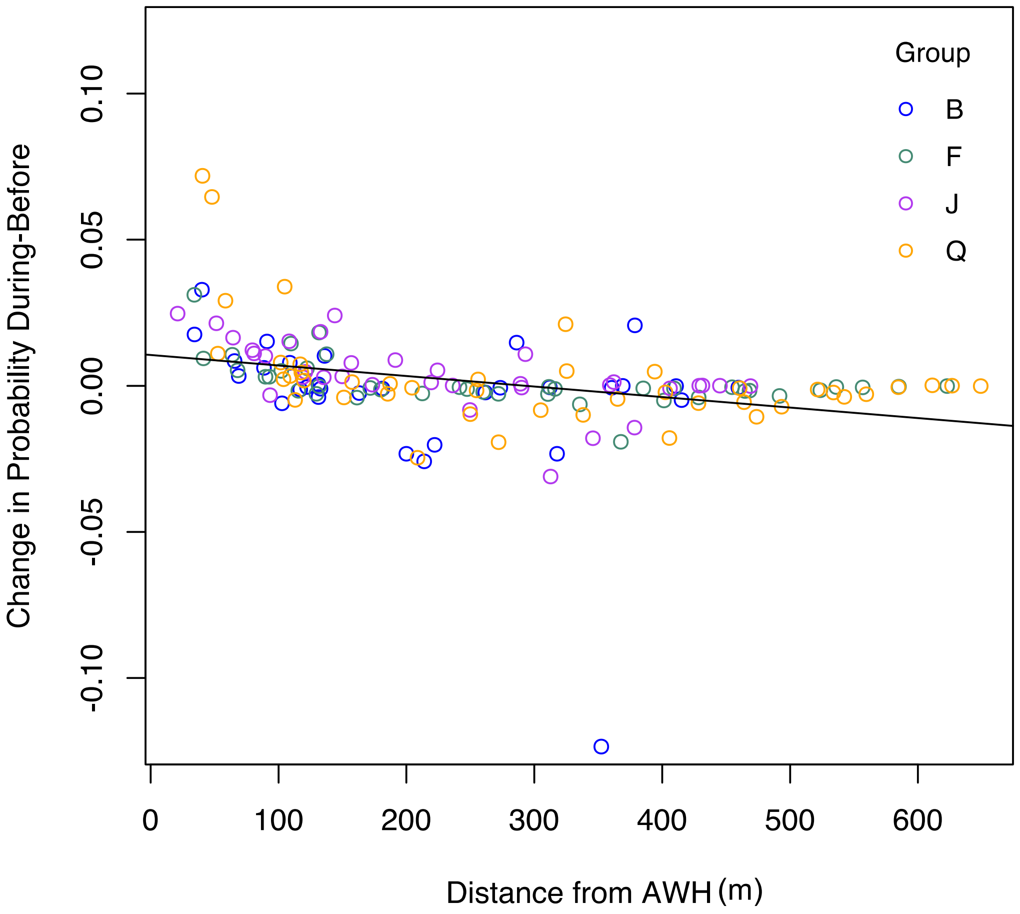

Figure 5. Change in probability at points along line between artificial waterhole (AWH) introduced in an experiment and habitually used natural waterhole before the experiment for four groups of red-fronted lemurs (*Eulemur rufifrons*) in Kirindy Forest, Madagascar, July-October 2017. Each point represents the change in probability at a given grid square in the area between a group's AWH and the natural waterhole the group previously used habitually.

Table 2: AIC scores for linear and null models of the change in probability of occupancy in only the grid cells that fall between two waterholes of interest. These are two waterholes that red-fronted lemurs (*Eulemur rufifrons)* used in Kirindy Forest, Madagascar during July-October 2017. Support for the linear model in the first subset (artificial waterhole, AWH-previous natural waterhole, NWH) indicates an increase in probability of occupancy in the areas where water was experimentally added, and a decrease in areas previously used for water. Support for the linear model in the second subset (NWH17-previous NWH) indicates a response to natural water drying: increased use of areas close to a remaining natural waterhole (NWH17), and decreased use of areas near the dried natural waterhole. Shaded cells indicate which model had the lower AIC score, or is more likely given the data. ΔAIC refers to the absolute value of the difference in AIC scores between the two models.

Subset of data	AIC Linear	AIC Null	ΔAIC
Points between AWH and previous NWH During-Before Experiment	-807	-800	7
Points between NWH17 and previous NWH After-Before Experiment	-583	-578	5

Analysis of the change in probability of occupancy after the experiment relative to before the experiment, focusing only on the points along the line between the natural waterhole used habitually before the experiment and the closest remaining natural waterhole after the experiment (NWH17), also revealed better support for a linear than null model (Table 2). Distance was a significant, though small, negative predictor of change in probability in this subset of the data, indicating that lemurs were more likely to spend time in the areas near NWH17 after the experiment than before the experiment (distance coefficient=-0.000044, $P<0.01$, t=-2.81, DF=101; Fig. 6, Table S1). In general, the lemurs were also less likely to spend time near their previously-used natural waterhole after than before the experiment. In other words, as a natural waterhole dried up, lemurs shifted their ranges away from this natural waterhole and toward a different natural waterhole that still contained water, suggesting that the presence of water was the primary reason for lemur groups to range here initially.

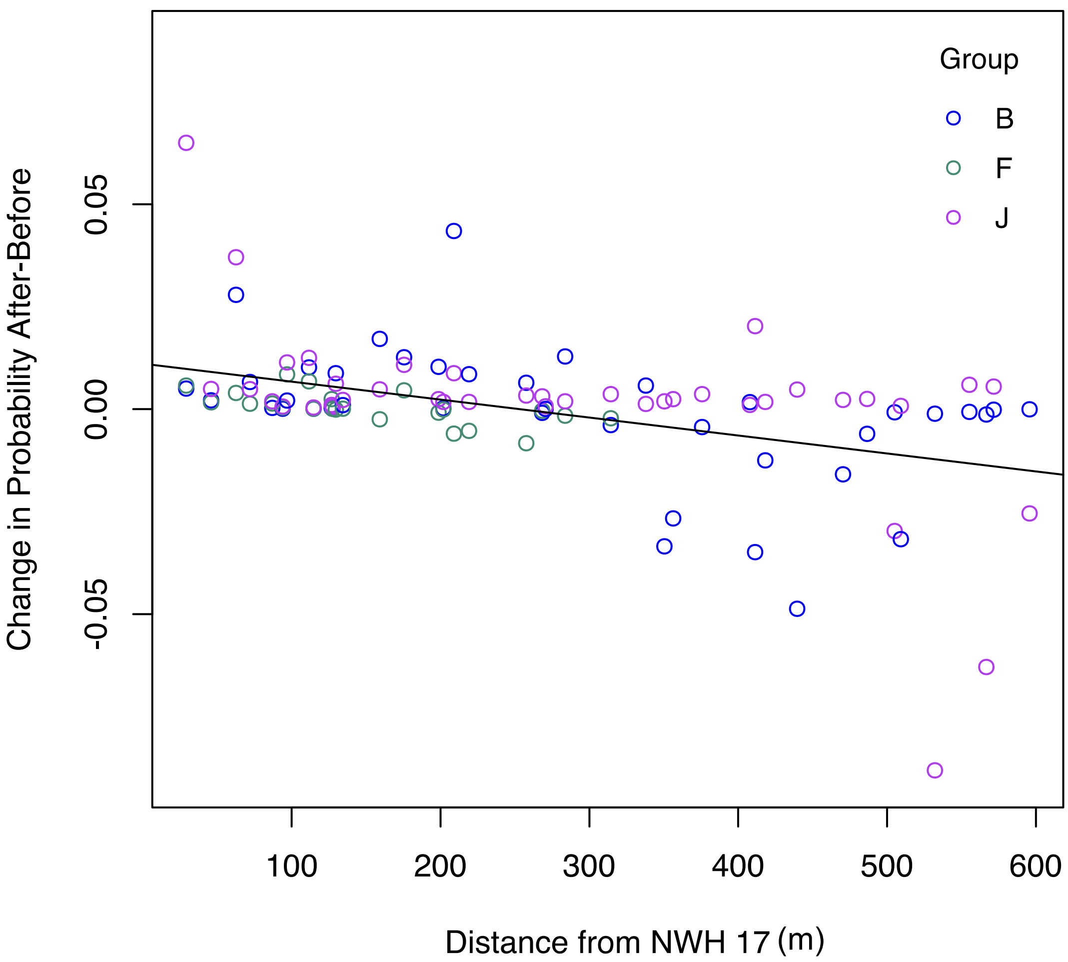

Figure 6. Change in probability at points between habitually used natural waterhole before an experiment and closest remaining natural waterhole (NWH17) after the experiment for three groups of red-fronted lemurs (*Eulemur rufifrons*) combined. These are two waterholes that red-fronted lemurs (*Eulemur rufifrons)* used in Kirindy Forest, Madagascar at the beginning and end of the dry season during July-October 2017. Lemur groups were more likely to spend time near NWH17, which was the closest remaining natural waterhole to these groups' home ranges at the end of the dry season, after the experiment. After the experiment, the groups were less likely to spend time in the areas near the natural waterhole that they habitually used before the experiment, where water was no longer available.

DISCUSSION

The main finding of this study is that the spatiotemporal availability of water can influence the habitat use patterns of a wild primate. Specifically, we demonstrated that experimental and natural changes in the distribution of water altered the boundaries of the area in which groups range and shifted the density of occupancy within the boundaries of the ranging area. Adding water to areas of the habitat resulted in increased intensity of ranging in these areas, and removal of the water caused a reduction of intensity of ranging. This pattern was observed in all groups except Group F, which did not reduce its intensity of ranging near the artificial waterhole after it had been removed. We assume this can be attributed to the artificial waterhole having been introduced into an area of the habitat that remained favorable for reasons independent of the presence of water. The sizes of the effect of the experiment (i.e. the coefficients for distance in the models) that we detected were relatively small, which may indicate a general consistency in areas of intense habitat use across experimental periods. Given our experimental approach, we are able to isolate the effects of water, and can conclude that water is a direct and important determinant of movement and habitat use in this species. Overall, these findings imply a high degree of behavioral flexibility in the areas ranged by our study groups as a function of accessing water resources.

As suggested by the case of Group F, patterns of habitat use are complex and likely respond to water availability, but also to other ecological factors, such as food availability, social context, and habitat suitability (Alba-Mejia et al. 2013; Clapp and Beck 2016; Crofoot 2013; Marshal et al. 2006; Poirotte et al. 2017; Rehnus et al. 2013; Viana et al. 2018). In addition, this study does not address inter-individual or inter-group variation in water intake or frequency of waterhole use, which could result from differences in water availability in food resources, availability of natural waterholes in groups’ home ranges, and individual life histories (Rosinger and Tanner 2015; Sapir et al. 2004; Tsurim et al. 2008), with the potential to lead to differences in the groups’ responses to the experiment. Although our experimental approach gives us more confidence in attributing specific importance to water for determining lemur ranging, experimental conditions cannot be perfectly controlled in wild populations. Given the noise introduced by other environmental changes (e.g. feeding trees) that likely influence lemur ranging, the strength with which our results support the influence of water is notable and suggests that water availability is an important driver of the ranging patterns of these lemur groups.

Previous observational evidence has supported that water can influence habitat selection in large mammalian herbivores (Bleich et al. 2010; Marshal et al. 2006; Purdon and van Aarde 2017) and primates (Barton et al. 1992; Campos and Fedigan 2009; Noser and Byrne 2014; Scholz and Kappeler 2004) living in arid habitats. The observational component of this study, which compared habitat use in the periods before and after our experiment, is consistent with these previous studies, but leaves open the possibility that some other factors might be driving changes in ranging patterns. However, the experimental approach of this study – introducing and removing water sources over a short time scale – provides a great deal of inferential power in terms of the effects of water on the behavior of dry-habitat living species that drink free water, and suggests that findings of associations between water availability and habitat use in other studies are likely to reflect causal relationships.

Our findings indicate that water distribution has a major impact on primate behavior. While this is known for large, terrestrial animals and species of economic importance, only a handful of studies have investigated the effects of water availability in various forms and distributions on primate behavior, and typically with observational or indirect methods rather than experimental approaches. For example, ring-tailed lemurs' (*Lemur catta*) ranges in an arid, semidesert scrub environment mapped onto the distribution of a food resource with high water content (Kelley, 2011, 2013). Similarly, provisioning of water made it possible for introduced, hybrid brown lemurs (*Eulemur* spp.) to live in Berenty Reserve, which would otherwise be too dry for them to survive (Jolly 2013; Pinkus et al. 2005). In combination with previous observational studies of the impacts of water on primate ranging (e.g. Barton et al. 1992; Dias et al. 2014; Scholz and Kappeler 2004), this study identifies an important, causative role for sources of water in the determination of primate habitat use, and suggests that future studies of primates should explicitly consider how water might impact behavior and ecology. Although we demonstrate large impacts of water distribution on the ranging patterns of a species known to frequently drink water, primate species with lower water requirements may still adjust their ranges subtly to meet their water needs. Given this evidence, distance from water sources is likely to be an important predictor of the geographic extents of many primate species, and may be an important variable to include in population size estimates and future projections (Herrera et al. 2018; Mercado Malabet and Colquhoun 2018).

Ranging behaviors are a clear choice of behavior to consider relative to water availability and distribution. This study also raises questions about how animals detect, locate, and keep track of the status of ephemeral water sources that vary across years. For example, in this study, the lemurs did not detect or use the artificial waterholes on their own for an entire week after introduction. That experimenter intervention was required for the lemurs to become aware of the water sources suggests that the lemurs either had to overcome their neophobia towards the artificial water sources or that an essential cue of the presence of water may have been missing in our artificial setup, or that memory may play an important role in determining the areas where search efforts are expended. Relatedly, research on elephants (*Loxodonta africana*) suggests that more experienced mothers may be more successful in supporting their calves through droughts in part because they remember the locations of critical water sources when others have dried up (Foley et al. 2008). In addition to the tasks of finding and remembering the locations of water, the lemurs must also navigate and coordinate group movements to water sources. In a previous study of this population, red-fronted lemurs responded to spatially separated drinking platforms by reducing group cohesion in transit to these platforms, suggesting consensus costs of group coordination in this context (Pyritz et al. 2013).

Variation in water quality may also influence habitat use, yet we have little understanding of the characteristics of water that are important to animals. For example, captive and wild lemurs prefer clean water to water that is contaminated with feces (Amoroso et al. 2017; Amoroso et al. 2019). It is possible that the concurrent manipulation of water quality (Amoroso et al. 2019) could have caused the lemurs to be either attracted to or repulsed by the different quality artificial water sources in the experiment, but anecdotally, we did not observe changes in the frequency of waterhole use across the duration of the experiment. Evidence in wild elephants suggests that they also prefer to avoid feces in their selection of water (Ndlovu et al. 2018). Many animals have been recorded to avoid feces and other cues of parasites in feeding contexts (Curtis 2014). Open questions include whether other wild animals exercise these same preferences for clean water, whether enough variation is present in naturally occurring water sources to exercise such preferences, and whether water scarcity might mediate these preferences. Studies on sensory ecology, group coordination, and parasite avoidance are thus logical next steps for investigating the impacts of water on animal behavior and evolution.

Our approach and findings provide a potential intervention for species facing unpredictability of water resources in the future, as global climate change brings with it more severe weather events, including possibly more droughts or longer periods of reduced rainfall (Desbureaux and Damania 2018; Schlaepfer et al. 2017; Trenberth et al. 2014). Changes to the distribution and quality of water sources may also be among the many complex impacts of more intensive human land use on ecosystems (Baker 2003; DeFries and Eshleman 2004; Jackson et al. 2001). In this study, lemurs proved to be highly flexible in their use of water resources in new areas of the habitat, suggesting that introducing artificial water sources may support survival through challenging times. However, more research is needed to understand the impacts of provisioning water for individual species and for ecosystems more broadly (Simpson et al. 2011).

In conclusion, we provide experimental evidence of the effects of water availability on wild primate ranging patterns. Undoubtedly, water ought to be an important factor in the ecologies of other wild animals in dry habitats. Future work could adapt this simple study design to determine whether these results are replicable in different species and habitats, and to understand the factors that influence variation in responses to water availability. Ultimately, water is expected to become an increasingly important factor for survival of many animals as a result of global climate change; thus, understanding the selective pressures exerted by water demands on animal behavior represents a high priority.

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SUPPLEMENTARY MATERIALS

Table S1. Model specifications for change in probability relative to AWH location for all points in each group's range. Exponential model formula is y = a * exp(b * x) + c, where y is the change in probability and x is the distance from the AWH. Null model formula is y = c. For corresponding plots, see Figures 3 and S1. Our dataset measured a change in probability, or the difference between two sets of probability values. We calculated these probabilities for over 300 grid squares, and the probabilities sum to 1, which explains the small values of the coefficients.

Group	**Time Period (Correlation str)**	**Model**	**Coefficient**	**Value**	**Std. Err.**	**t-value**	**p-value**	**Resid DF**
B	During-Before (Spherical)	Exponential	a	0.05307225	0.02418182	2.1947171	0.0288	352
			b	-0.0236586	0.00819534	-2.8868303	0.0041	
			c	-9.455E-05	0.00041977	-0.2252296	0.8219	
		Null	c	-1.00E-05	0.00041299	-0.0242138	0.9807	354
	After-During (Linear)	Exponential	a	-0.049572	0.01495683	-3.314336	0.001	355
			b	-0.0183499	0.00463273	-3.96092	0.0001	
			c	0.00050948	0.0004464	1.141308	0.2545	
		Null	c	-1.00E-05	0.00094389	-0.0105945	0.9916	357
F	During-Before (Gaussian)	Exponential	a	0.06314328	0.02586691	2.441083	0.0151	377
			b	-0.0291585	0.00877684	-3.322212	0.001	
			c	-0.0002316	0.00033325	-0.69505	0.4875	
		Null	c	2.16E-06	0.00036395	0.00592763	0.9953	379
	After-During (Linear)	Exponential	a	-15.592042	2150960147	0	1	377
			b	-0.613537	3970398	-0.0000002	1	
			c	-0.000541	0	-0.8469923	0.3975	
		Null	c	2.50E-06	0.00063589	0.00392909	0.9969	379
J	During-Before (Linear)	Exponential	a	0.0351585	0.01071492	3.281264	0.0011	328
			b	-0.0120587	0.00343072	-3.514906	0.0005	
			c	-0.0009081	0.00066849	-1.358443	0.1753	
		Null	c	8.43E-06	0.00060553	0.01392458	0.9889	330
	After-During (Linear)	Exponential	a	-0.0021915	0.00587242	-0.3731888	0.7092	376
			b	-0.0097141	0.02503823	-0.3879715	0.6983	
			c	0.00025112	0.00043023	0.583691	0.5598	
		Null	c	0	0.00068461	0	1	378
Q	During-Before (Linear)	Exponential	a	0.11637999	0.01395089	8.342121	0	403
			b	-0.0170795	0.0016897	-10.108028	0	
			c	0.00071691	0.00039837	1.799621	0.0727	
		Null	c	5.91E-06	0.00045058	0.01310539	0.9896	405
	After-During	Exponential	a	-0.0771763	0.01255851	-6.145337	0	403

(Linear)		b	-0.0157609	0.00214873	-7.334972	0	
		c	-0.0010331	0.00040327	-2.561664	0.0108	
	Null	c	4.83E-05	0.00073091	0.06611785	0.9473	405

Table S2. Model specifications for change in probability relative to artificial waterhole or NWH17 and location of points along the line between waterholes. An exponential correlation structure was used. Our dataset measured a change in probability, or the difference between two sets of probability values. We calculated these probabilities for over 100 grid squares, and the probabilities sum to 1, which explains the small values of the coefficients.

Subset of data	Model	Coefficients	Value	Std.Error	t-value	p-value	Resid DF
Points between AWH-previous NWH	Linear	Intercept	0.01043734	0.00325838	3.203227	0.0017	146
		Distance	-3.54E-05	1.0435E-05	-3.392053	0.0009	
	Null	Intercept	0.00089821	0.00220723	0.4069379	0.6846	147
Points between NWH17-previous NWH	Linear	Intercept	0.01113211	0.00456547	2.438328	0.0165	103
		Distance	-4.39E-05	1.4356E-05	-3.058313	0.0028	
	Null	Intercept	-0.0008372	0.00341153	-0.2454081	0.8066	104

Figure 1

Figure 2

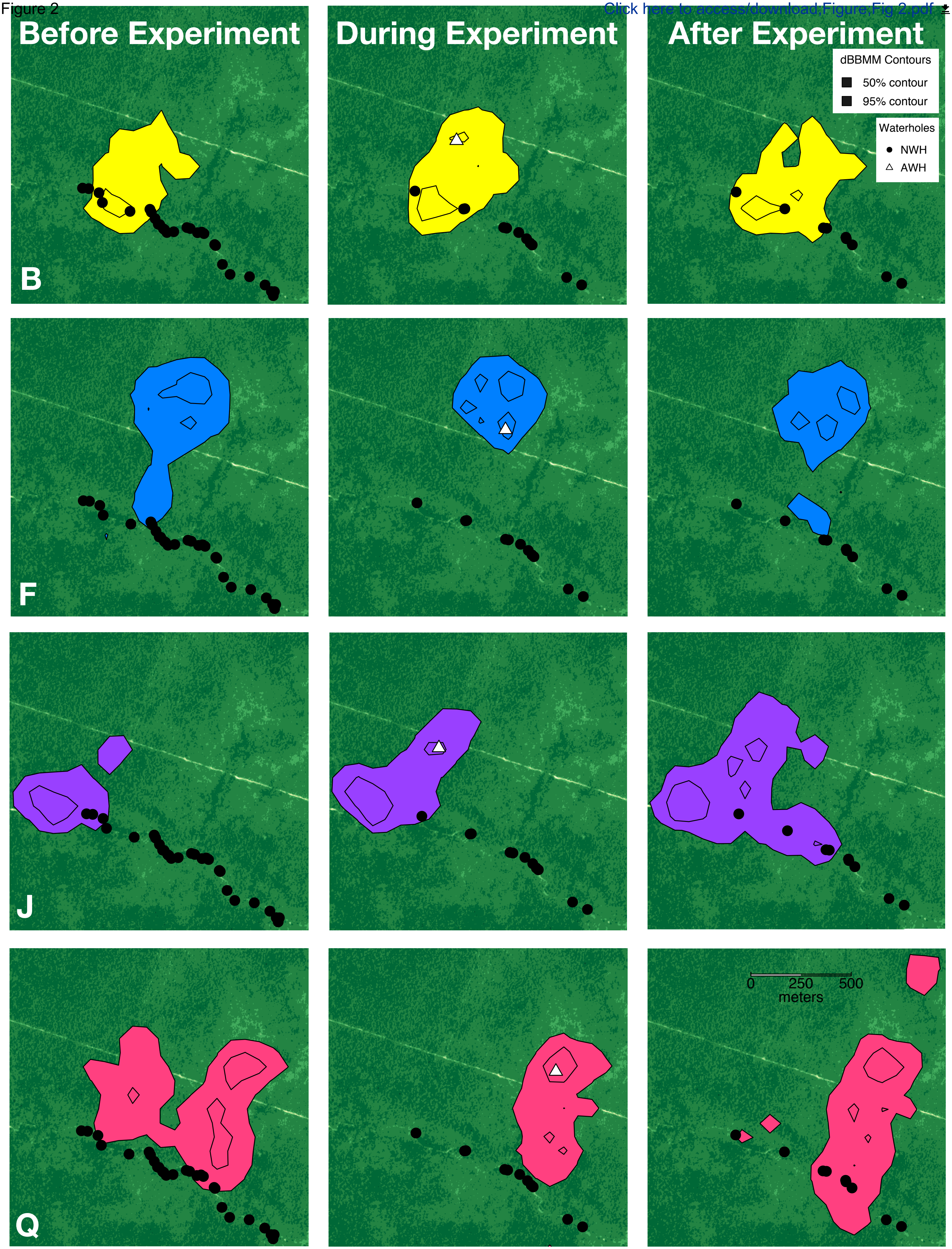

Before Experiment
During Experiment
After Experiment
dBBMM Contours
■ 50% contour
■ 95% contour
Waterholes
● NWH
△ AWH
B
F
J
Q
0
250
500
meters

Figure 3

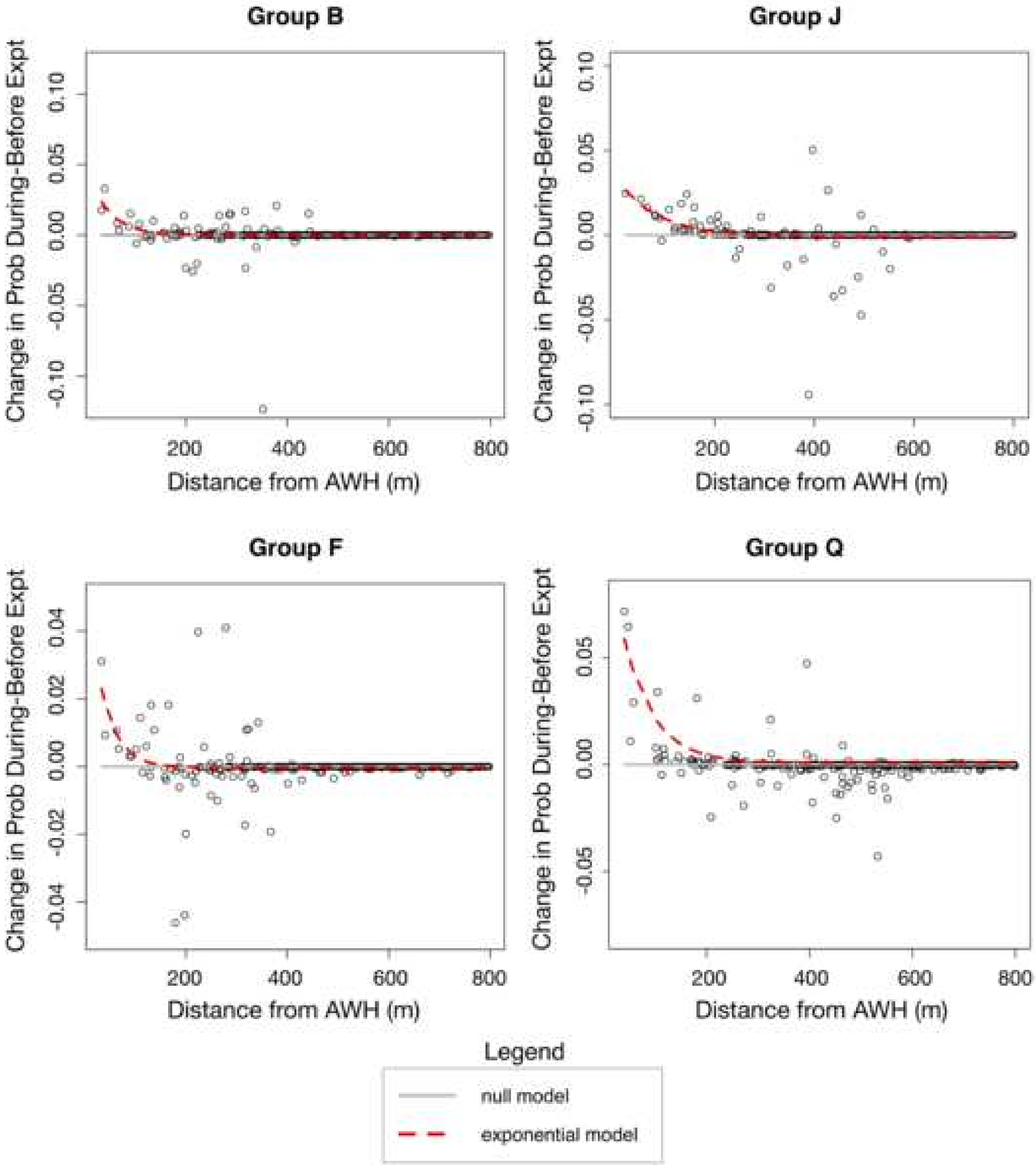
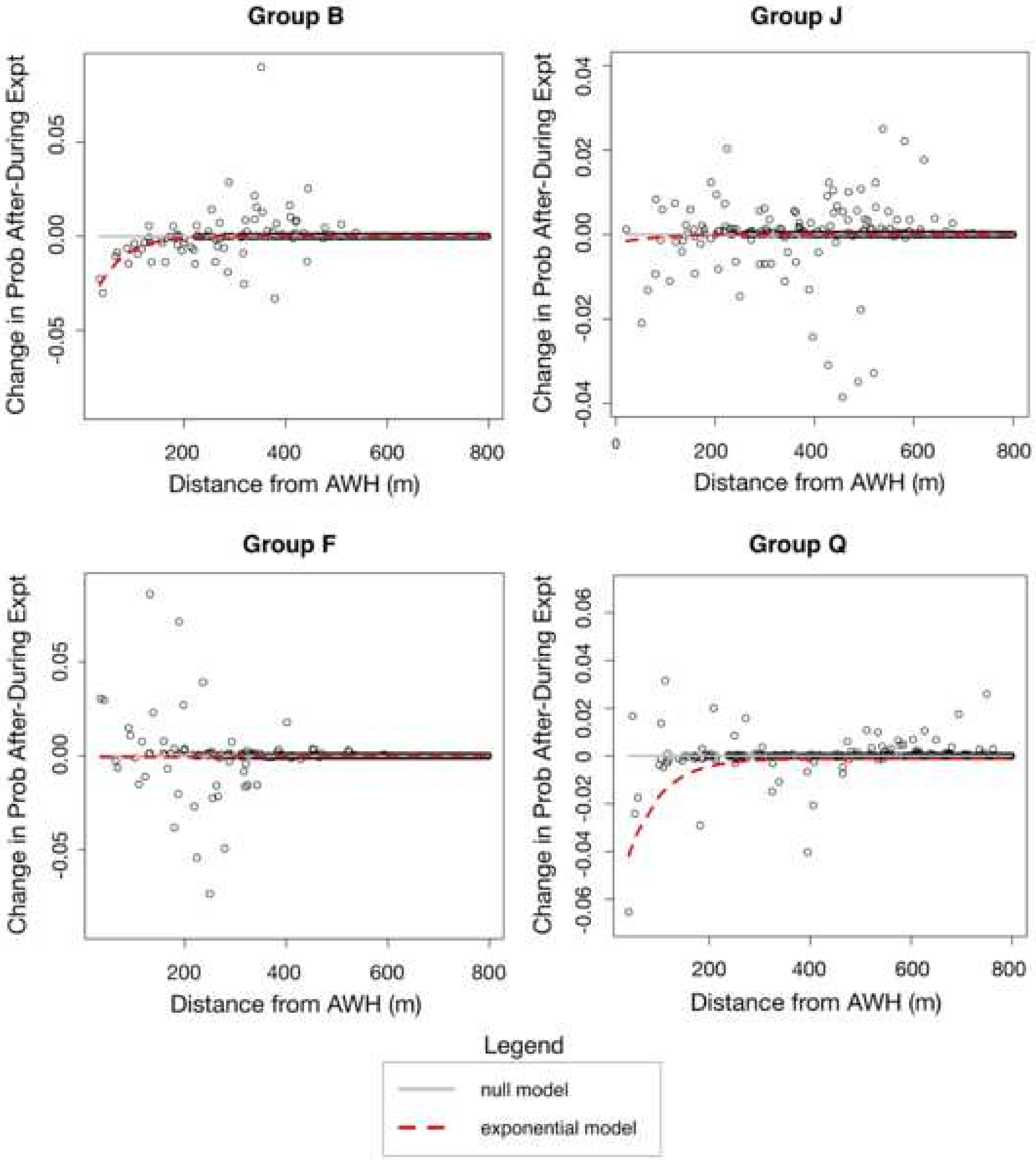
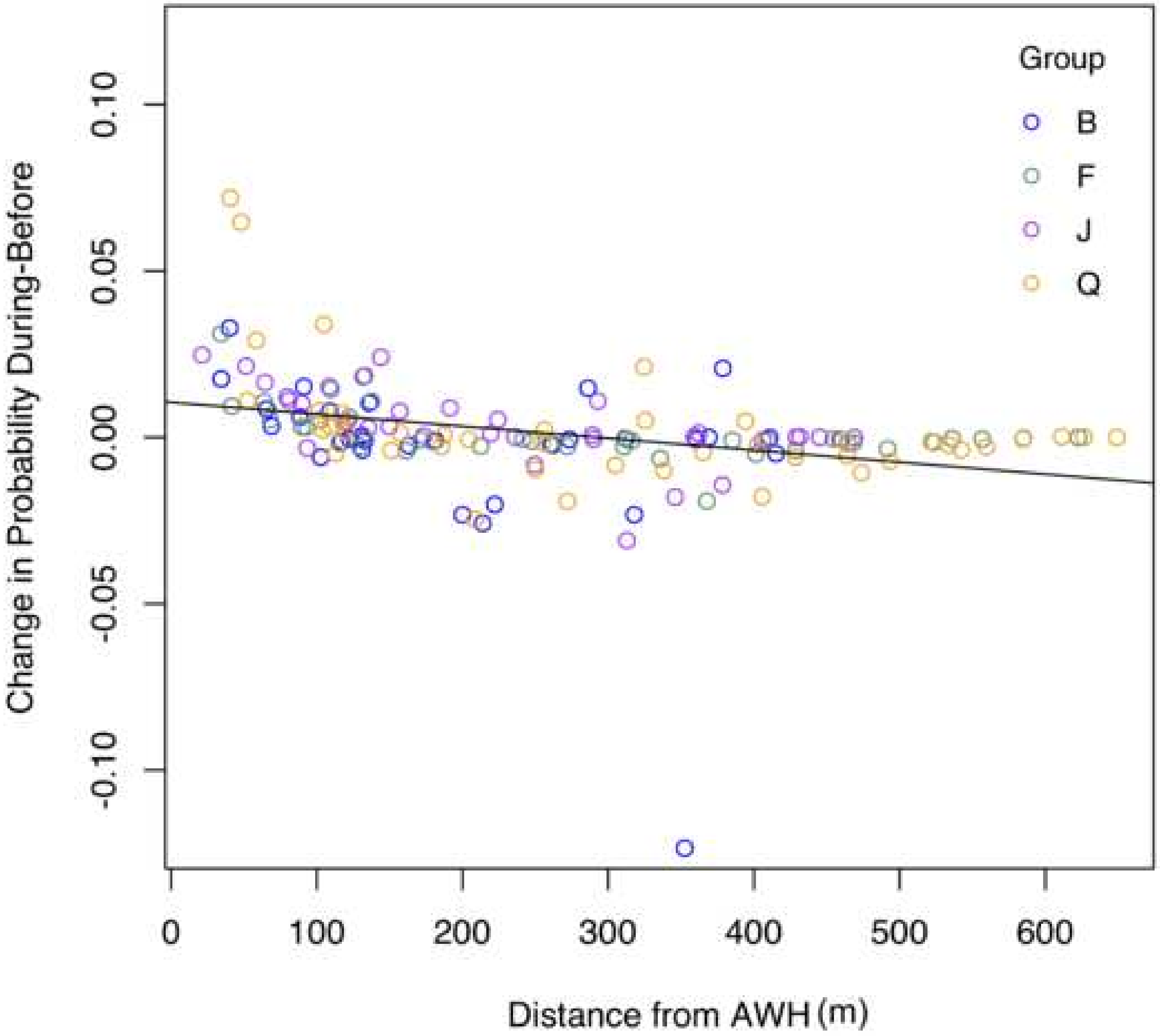
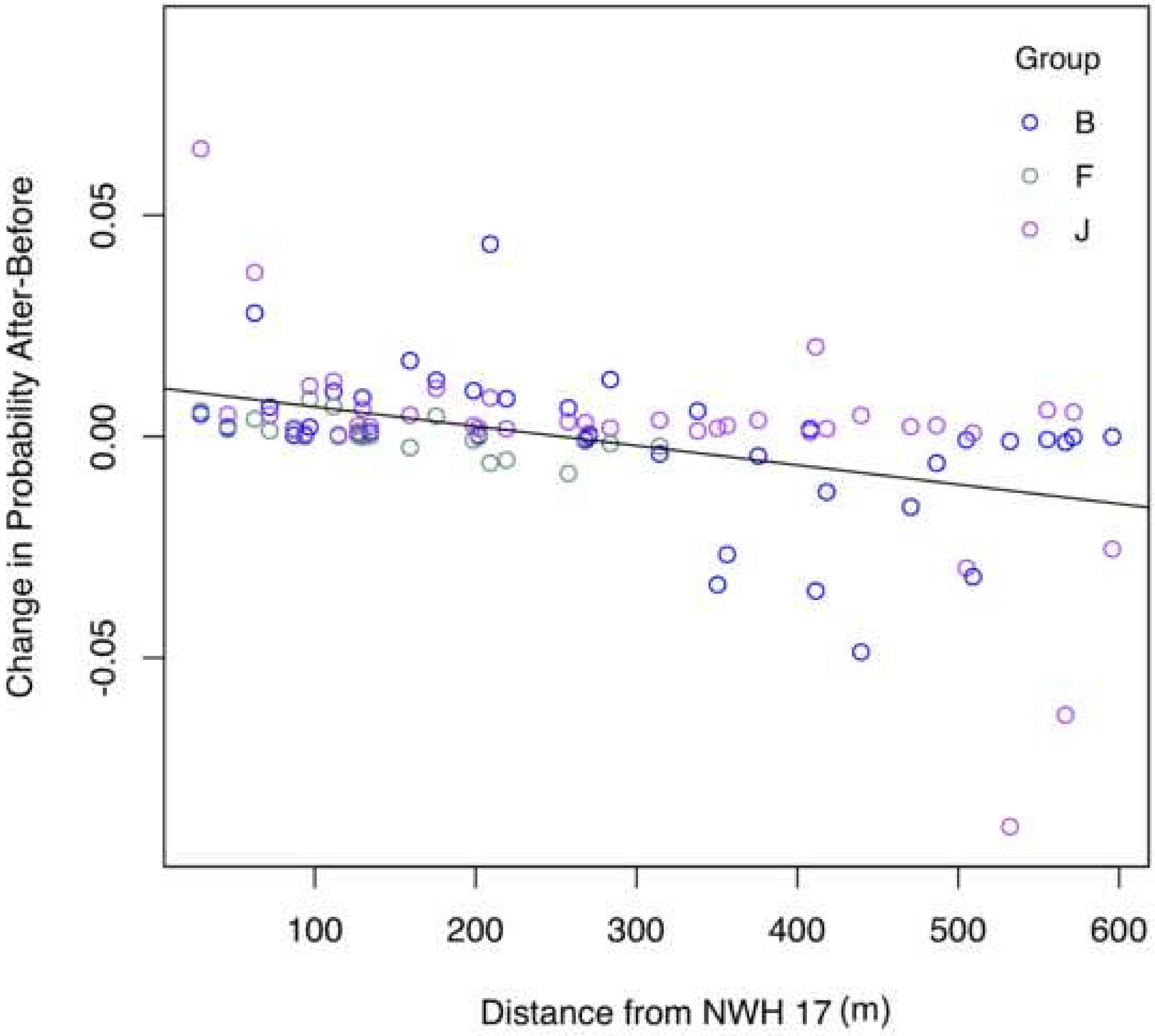

Group B
Group J
Group F
Group Q
Change in Prob During-Before Expt
Distance from AWH (m)
0.10
0.05
0.00
-0.05
-0.10
0.04
0.02
0.00
-0.02
-0.04
200
400
600
800
Legend
null model
exponential model

Figure 4


Group B
Change in Prob After-During Expt
0.05
0.00
-0.05
200
400
600
800
Distance from AWH (m)
Group J
Change in Prob After-During Expt
0.04
0.02
0.00
-0.02
-0.04
0
200
400
600
800
Distance from AWH (m)
Group F
Change in Prob After-During Expt
0.05
0.00
-0.05
200
400
600
800
Distance from AWH (m)
Group Q
Change in Prob After-During Expt
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
200
400
600
800
Distance from AWH (m)
Legend
null model
exponential model


Group
○ B
○ F
○ J
○ Q
Change in Probability During-Before
0.10
0.05
0.00
-0.05
-0.10
0
100
200
300
400
500
600
Distance from AWH (m)


Group
B
F
J
0.05
0.00
-0.05
100
200
300
400
500
600
Change in Probability After-Before
Distance from NWH 17 (m)