



## Movement ecology in a captive environment: the effects of ground substrate on movement paths of captive rhesus macaques, *Macaca mulatta*

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Movement ecology is a growing field, and an important component of movement ecology is investigating how environmental factors influence animal movements. The structure of food resources, such as density and distribution, has been shown to influence the speed, distance and tortuosity of animal paths. We investigated the influence of the type of ground substrate on the movement paths of groups of captive rhesus macaques. Grass substrate provides supplementary food resources (e.g. insects, blades of grass) having more random and unpredictable distribution and higher density relative to gravel substrate, which is more depauperate in supplemental foods. Adult females in four grass enclosures travelled along more tortuous paths, as measured by higher frequency of changes in direction and stops and a smaller straightness index compared to adult females in two gravel enclosures. These results were largely replicated in a group that was moved from an enclosure with gravel to one with grass. Dominance rank further influenced tortuosity within enclosures with gravel substrate: higher-ranking animals showed less tortuous paths and shorter total distances than lower-ranking animals. Additionally, movement bouts in which the apparent goal was feeding on monkey chow were faster (regardless of substrate) and longer (in enclosures with grass substrate) compared to movement bouts in which the apparent goal was foraging for supplemental foods. Captive macaques, like free-ranging animals, move along more tortuous paths and at slower speeds when their food resources are randomly distributed and high in density.

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Movement ecology is a growing field of study (Holyoak et al. 2008). A primary focus of this emerging discipline is to investigate how environmental factors such as food influence animal movements (Nathan et al. 2008). Movement ecology integrates multiple approaches in its attempts to understand how and why animals move through their environments. Optimal foraging theory is particularly useful as it combines movements with efficiency of time or energy, both of which can affect reproductive success of individuals. Thus, according to optimal foraging theory, animals are adapted to travel the route of least effort between resources because time and/or energy are limited (Pianka 1988) and foraging efficiency may be optimized by travelling directly to food resources. For food resources that are not detectable by the senses at the outset of travel, foraging efficiency can be maintained or improved by prior knowledge of the locations of food resources (Noser & Byrne 2007). With such knowledge, individuals can increase travel speed.

### Speed and Tortuosity in Relation to Predictability of Resources

Speed has long been thought to indicate learning (Logan 1982). An individual that travels both quickly and directly to a resource is assumed to have learned and remembered the location of that resource (Pochron 2001). The movements of baboons (*Papio hamadrayas cynocephalus* and *P. h. ursinus*) are consistent with this assumption. Baboons move quickly and along straighter paths to foods that are important to their diet and predictable in location (Pochron 2001; Noser & Byrne 2007). Among mangabeys (*Cercocebus atys* and *Lophocebus albigena*), speed of travel is faster to trees in which individuals ate fruit the previous day (Janmaat et al. 2006). In summary, the values of these travel characteristics provide a way of measuring animal decision making that cannot otherwise be known.

Animals are thought to have spatial memory for at least some of their resources, because animals frequently return to the same sleeping sites (Rosalino et al. 2005; Noser & Byrne 2007), latrines (Loureiro et al. 2007), water holes and predictable food resources that make up a significant proportion of the diet (Garber 1989; Janson 1998; Cunningham & Janson 2007). Animals often travel long distances to reach many of these resources even when they

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cannot see the resource at the outset of travel (Pochron 2001; Noser & Byrne 2007).

Many foods are not predictable, however, in either space or time. The locations of ephemeral plant foods and mobile insects, for instance, can change quickly over time (Terborgh 1983; Janson 1996). It may be neither possible nor useful to memorize the locations of such unpredictable food resources. Therefore, some foods will be encountered unexpectedly.

Animals searching for unpredictably located foods are not expected to use a direct and rapid route to their foods but are expected to increase the tortuosity of travel (Crist et al. 1992; McIntyre & Wiens 1999; Pochron 2001). The degree of path tortuosity estimates how efficient animals are in their search for an apparent goal (Benhamou 2004), whether or not animals are travelling towards a known goal (Noser & Byrne 2007) and whether or not members of a given species have the capacity to search for and utilize unpredictable or unknown food resources (Isbell 2004).

#### *Tortuosity in Relation to Resource Distribution and Density*

Animals often appear to adjust their movement patterns during foraging depending upon the distribution, density and heterogeneity of the food resources. When food distribution is uniform or random, animals frequently increase the tortuosity of their paths. Bumblebees, *Bombus occidentalis*, white-tailed deer, *Odocoileus virginianus*, darkling beetles, *Eleodes extricata*, and grey teal ducks, *Anas gracilis*, for example, all show more tortuous travel paths when foraging in habitats with uniformly or randomly distributed food resources as opposed to habitats with food resources that are clumped or patchily distributed (Cartar & Real 1997; Etzenhouser et al. 1998; McIntyre & Wiens 1999; Roshier et al. 2008). Food-deprived beetles travel along more tortuous paths when foods are randomly distributed, whereas satiated beetles, for which foraging efficiency is assumed to be less important, travel along much straighter paths (McIntyre & Wiens 1999). Thus, tortuous movements may constitute the optimal foraging strategy under conditions of random or unpredictable food distribution. Similarly, in higher-quality habitats where food resources occur at higher densities, both beetles (*Eleodes* spp.) and goats travel along more tortuous paths (Crist et al. 1992; de Knecht et al. 2007). When foods are at high density, it may be neither possible nor necessary to remember the location of a food resource.

#### *Social Factors and Animal Movements*

Social factors such as group size and the presence of clearly defined dominance relationships have also been found to affect movements among African elephants, *Loxodonta africana*, and many of the more frugivorous Old World monkeys (Isbell 1991; Janson & Goldsmith 1995; Wittemyer et al. 2007). For example, in vervets (*Cercopithecus aethiops*), macaques (*Macaca* spp.) and mangabeys, which have well-defined female dominance hierarchies, individuals in larger groups may travel further per day, split into foraging subgroups, or increase interindividual distances (Waser 1977; Isbell 1991; Isbell et al. 1999a). Lower-ranking females may also be more constrained in their movements than higher-ranking females, particularly as groups become larger (Isbell et al. 1999a; Chancellor & Isbell 2009). At the same time, how individuals move may also influence the extent of group cohesion and the potential for developing social alliances within groups. For example, compared to vervets, individual patas monkeys, *Erythrocebus patas*, move less tortuously over short periods of time (30 min) while also moving more laterally or at greater angles relative to the group's centre of mass. Such

movements increase the independence of individuals relative to others in the group and reduces opportunities for subgroup and alliance formation (Isbell et al. 1999b). Thus, investigations into the movement ecology of animals that live in groups will also benefit from including potential influences of social factors on individual movements.

#### *Manipulation of Animal Movements in Captivity*

Although captive animals are limited in their movements by the dimensions of their enclosures and therefore are expected to show a greater degree of tortuosity than their wild counterparts regardless of the density and distribution of food resources, captivity provides a good opportunity to investigate movement ecology because one can more easily control food characteristics than is possible in the wild. For instance, in captive groups of primates, the majority of their food (monkey chow) is predictable in both space and time (Bloomsmith & Lambeth 1995). This is typical also at the California National Primate Research Center (CNPRC), where groups of rhesus macaques live in large outdoor enclosures and are fed the same amount of food at the same time and location (food hoppers on a cement platform) every day. However, groups at the CNPRC do differ in the type of ground cover in their enclosures. Macaques living in enclosures with gravel as the ground substrate have an environment that is relatively depauperate in supplementary foods (Beisner & Isbell 2008) whereas macaques living in enclosures with grass as the ground substrate have an alternative food resource (Goldstein & Richard 1989) that also hosts insects and other arthropods, another alternative food resource. Indeed, macaques living in enclosures with grass substrate spend more time engaged in foraging behaviour than macaques living in enclosures with gravel substrate (Beisner & Isbell 2008), suggesting that ground substrate may influence the distribution, density and predictability of supplemental food resources, and therefore, the movement patterns of individuals.

Grass substrate creates a more complex captive environment in which to forage compared to gravel. For example, insects that live in grassy environments may not be predictable in location and also may not be readily visible until in close proximity. Moreover, if animals forage for blades of grass by selecting particular blades (e.g. preferring new blades of grass over mature blades of grass), then grass itself may be unpredictable in its distribution. Thus, animals may know that blades of grass and arthropods are available in the enclosure, but the exact locations of these resources may be unknown, and thus unpredictable. Drawing on the hypothesis that movements are adjusted to the predictability, density or distribution of food resources, one aim of this study was to test the prediction that animals in enclosures with grass substrate would move more tortuously as they foraged than animals in enclosures with gravel substrate.

A corollary aim was to determine whether movements to a known food location (the monkey chow hopper) is more often associated with purposeful movement, whereas foraging for less predictable foods is more often associated with opportunistic movements. Purposeful movement is characterized by faster speed and more direct travel, whereas opportunistic movement is slower and more tortuous. Regardless of the type of ground cover, movement bouts whose apparent goal is foraging for supplemental foods are predicted to be slower and shorter, whereas movement bouts whose apparent goal is feeding on monkey chow are predicted to be faster and longer (Pochron 2001).

Since rhesus macaques are group-living animals with clearly defined dominance hierarchies among females, we also predicted that rank would influence movement patterns. We tested the

prediction that lower-ranking animals would show more tortuous paths and that they would travel longer total distances than higher-ranking females. The predictions were based on the supposition that lower-ranking females are less efficient in their movements as a constraint of their social environment, perhaps as a result of more frequent displacements by higher-ranking females from known food locations, leading to increased foraging for alternative food resources. Finally, we tested the prediction that females in larger groups would travel longer total distances than females in smaller groups.

## METHODS

### *Study Site and Groups*

The study was conducted at the California National Primate Research Center (CNPRC) in Davis, CA from September 2006 to August 2007. The subjects of this study were seven groups (Groups 1, 2, 5, 8, 14, 16 and 18) of rhesus macaques housed in 0.2 ha (60 × 30 m) enclosures (Table 1).

Four groups had naturally growing grass in their enclosures (at least 30% grass of the 0.2 ha area) and three groups had gravel/dirt substrate with no grass. Grass substrate consisted of grass patches that varied over the study period as a result of seasonal changes in temperature and rainfall as well as macaque foraging behaviour. Grass ranged in height from very short to approximately 15 cm. Gravel substrate consisted of small, grey pebbles spread over most of the enclosure. Supplemental foods that macaques were observed eating included blades and roots of grass (grass substrate only), provisioned sunflower seeds, arthropods and dirt. Enclosures were otherwise similar in having 10 A-frame houses, multiple suspended barrels, swings and several perches. Monkey chow was given to each group at approximately 0700 hours every morning and again between 1430 and 1530 hours in the afternoon, always in the same location. Monkey chow was typically available throughout the day because groups usually do not eat all of the chow that is given. Additionally, either fresh fruits/vegetables or a seed mixture (supplemental food resources) were scattered throughout the enclosures every morning.

One group (Group 2) began the study in a gravel enclosure and was moved to a grass enclosure (30% grass coverage) after 7 months. Group 2 therefore provides a unique opportunity to compare movement patterns of the same animals in both grass and gravel substrates.

Rhesus macaques in this outdoor colony were managed with a minimal level of disturbance, and individuals of each group were free to interact with one another as they chose. Disturbances within the enclosure were typically limited to daily morning health checks, four round-ups per year to conduct health examinations on all animals and removal of injured or sick animals for medical treatment.

### *Sampling Methods*

A scaled map was constructed of the enclosure's two-dimensional ground space. Since all enclosures had the same dimensions, the same map was used for all enclosures. Vertical poles spaced 6 m apart throughout the enclosures helped delineate the paths of movement plotted by the first author (B.A.B.) of 172 adult females in seven groups during 222 20-minute focal samples over 147 days during a 12-month period. The number of focal samples collected from each group ranged from 29 to 32.

Focal subjects were chosen according to the following criteria: (1) only adult females were observed (4 years and older); (2) subject was on the ground, as animals sitting on perches or A-frames were less likely to move about the enclosure; (3) subject was stationary long enough to plot her position on the scaled map of the enclosure; and (4) subject was not engaged in social grooming or huddling. Once begun, focal samples continued regardless of focal animal behaviour. Focal samples containing aggressive chases or those disrupted by human activity were not, however, included in analyses. Preference was also given to adult females that had not been sampled previously. For each group, between four and seven individuals were observed more than once, but none more than three times.

Relative dominance ranks were obtained from records of weekly behavioural observations of displacements and aggressive interactions conducted by the behavioural management staff. Females were divided into three rank categories: high, middle or low, based on whether they were in the top, middle or bottom third of the dominance hierarchy, respectively. Those females in the exact middle of two categories were placed in the lower of the two rank categories.

One group was observed each day between 0800 and 1700 hours on a rotating schedule, such that each of the seven groups was observed once every 2 weeks. B.A.B. conducted two 20 min focal samples each day, either in the morning (0800–1100 hours) or the late afternoon (1500–1700 hours) when the groups were more active.

During each focal sample, B.A.B. plotted the exact path of movement each time the focal subject moved. Movement was defined as walking or running a minimum of two steps in the horizontal plane, and a stop was defined as sitting down or standing still for at least 2 s. Vertical movement was not recorded. The movement between each starting point and stopping point is referred to here as a movement bout. A lap-counter stopwatch was used to measure the duration of each movement bout and each period of nonlocomotor activity.

The following variables were measured to estimate the tortuosity of an animal's path of movement: total distance moved, straight-line distance moved (straight line drawn between the subject's location at the beginning and at the end of the focal sample), the number of times the focal subject stopped, the number of times the focal subject changed direction and the ratio of the

**Table 1**  
Characteristics of rhesus macaque study groups

Group	Substrate	Group size*	Adult sex ratio M:F	Focal animals
1	Grass	141 (129–156)	1:3.2	24
2	Both†	155 (141–180)	1:3.1	25
5	Grass	170 (160–187)	1:5.2	23
8	Gravel	164 (156–180)	1:3.8	28
14	Grass	88 (78–102)	1:7.8	21
16	Grass	134 (122–146)	1:7.8	24
18	Gravel	140 (123–158)	1:4.5	27

\* Means (ranges in parentheses).

† Group 2 was moved to an enclosure with grass ground substrate after 7 months.

straight-line distance to the total distance (Batschelet 1981), referred to here as the straightness index. This index measures the degree to which an animal's path deviates from a straight line and is a good measure of the efficiency of directed paths (Benhamou 2004).

We included two additional measures to estimate path tortuosity, frequency of stops and changes in direction (per focal hour), because the straightness index is a less accurate estimate of tortuosity for random movement paths than it is for directed paths (Benhamou 2004). A change in direction was defined as a turn of at least 45° (similar to changing the direction of travel from north to northwest); only such obvious changes in direction were counted because of the likely error in recording fine-scale features of animals' movement paths. Additionally, the focal animal had to move a minimum of two steps in a new direction to be recorded as a change in direction. The number of changes in direction is a simple and intuitive measure of the extent of convolution in an animal's movement path.

The number of stops in a movement path was counted to measure how frequently individuals encounter unexpected resources or reassess their location with respect to a desired resource. Individuals that stop more frequently may be doing so because resources are available at higher densities or resources are located in unpredictable locations. Focal animal behaviour was recorded at all stopping locations, including whether or not feeding occurred (moving hand from substrate to mouth).

We also calculated the distance and speed (m/s) of movement bouts within focal samples, and categorized movement bouts with respect to their apparent goal (i.e. feeding on monkey chow or foraging for supplemental foods). We expected movement bout speed to vary by the predictability of a food resource, such that movement bouts would be slower when macaques were searching for supplemental foods and faster when they were moving towards the monkey chow. We reasoned that the behaviour shown at the end of a movement bout was likely to be the goal of the movement.

### Statistical Analyses

We analysed the data using linear and generalized linear mixed-effects regression models. Models were fitted to the data on the following dependent variables: total distance, frequency of changes in direction, frequency of stops, straightness index, movement bout distance and movement bout speed. We ran a series of models for each dependent variable using a stepwise procedure where a single predictor or interaction term was added to the model at each step. Akaike's Information Criterion (AIC) scores were used to select the best fit model (i.e. the model with the lowest AIC score). Following the recommendation of Burnham & Anderson (2002), nested models having a difference in AIC score less than or equal to two

( $\Delta\text{AIC} \leq 2$ ) were considered equivalent. For travel path characteristics (i.e. total distance, frequency of stops, changes in direction and straightness index), fixed effects included substrate type, female rank and group size. For movement bout characteristics (i.e. bout distance and speed), fixed effects included the apparent goal of the movement bout and substrate type. A random effect for female was included in the linear regression and Poisson models. However, random effects were not possible for the gamma family models; thus, average values per female were the data for these models. The random effect for group was quite small for all models and was excluded from further analyses.

Generalized linear models were fitted to the dependent variables frequency of stops and changes in direction per hour (Poisson distribution) as well as to total distance per hour and straightness index (gamma distribution) (McCullagh & Nelder 1989). Prior to fitting linear regression models, we log-transformed the dependent variables movement bout distance and speed. Because of small sample size, we used nonparametric tests to evaluate the travel paths and movement bouts for animals in Group 2, the group that was moved from an enclosure with grass to one with gravel. All analyses were performed using the R statistical computing program (R Development Core Team 2008) and Stata 9 (Stata Corp., College Station, TX, U.S.A.).

Means and standard errors of all variables are presented in Tables 2 and 4. Some individuals were sampled more than others, and thus, means and standard errors were calculated using the median values for each individual to ensure equal representation of all sampled individuals (i.e. one value per individual).

## RESULTS

### Travel Paths

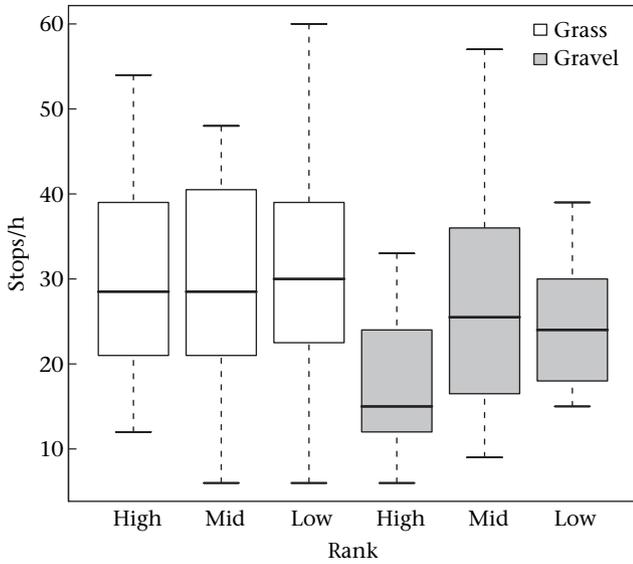
For number of stops per hour, the best fit model included fixed effects for substrate, rank and the interaction term substrate  $\times$  rank (compared with the second best model,  $\Delta\text{AIC} = 5$ ). As predicted, animals in grass enclosures stopped more frequently (mean = 31.6 stops/h) than animals in gravel enclosures (23.6 stops/h;  $P < 0.001$ ). Rank had a significant effect only on enclosures with gravel. In those enclosures, high-ranking females stopped less frequently than mid-ranking ( $P = 0.05$ ) and low-ranking ( $P = 0.003$ ) females ( $N = 190$ ; Table 2, Fig. 1). The linear prediction for females in gravel was 16.8, 26.7 and 25.3 stops/h for high-, mid- and low-ranking females, respectively, whereas the linear prediction for females in grass was 30.2, 29.9 and 33.1 stops/h for high-, mid- and low-ranking females, respectively.

For number of direction changes per hour, the best fit model included fixed effects for substrate, rank and the interaction term substrate  $\times$  rank (compared with the second best model,

**Table 2**  
Means and standard errors per focal hour are shown for all travel path characteristics for all groups of rhesus macaques

Condition	Group	Total distance	Straightness	Stops	Change direction
Gravel	8	205.1±23.6	0.50±0.05	24.8±2.1	19.2±2.3
Gravel	18	203.1±30.6	0.51±0.05	22.5±2.0	18.8±2.4
Overall gravel	8, 18	204.1±19.2	0.51±0.04	23.6±1.5	19.0 ± 1.6
Grass	1	219.9±23.2	0.39±0.04	31.4±2.3	37.2±3.2
Grass	5	182.2±20.4	0.37±0.05	30.0±2.9	32.6±3.9
Grass	14	241.9±24.2	0.27±0.04	35.1±2.1	41.2±2.9
Grass	16	194.2±22.3	0.36±0.05	30.0±2.6	35.1±3.7
Overall grass	1, 5, 4, 16	209.3±11.4	0.34±0.02	31.6±1.2	36.5±1.7
Gravel (7 months)	2	203.6±31.4	0.39±0.05	24.2±2.6	17.6±2.7
Grass (7 months)	2	193.5±29.8	0.36±0.05	34.6±3.7	37.4±4.9

The median values for each individual were used to calculate the means and standard errors of travel path characteristics to ensure equal representation of all sampled individuals. Most individuals were sampled only once, but four to seven individuals per group were sampled multiple times. All distances were measured in m/h.



**Figure 1.** Frequency of stops per hour for rhesus macaques in each rank and substrate category. The number of times individuals stopped/h for all sampled individuals' travel paths per rank category per substrate (grass:  $N = 38, 40, 48$  for high, mid and low rank; gravel:  $N = 18, 20, 26$  for high, mid and low rank). Boxes represent the interquartile range and the black bar is the median number of stops/h. The upper (and lower) whiskers are drawn to the largest (or smallest) data point not lying above the 75th percentile (or below the 25th percentile) +  $1.5 \times$  IQR.

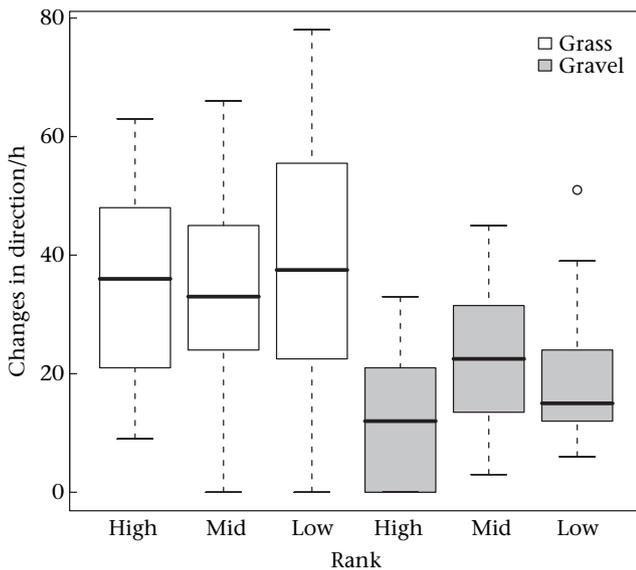
$\Delta$ AIC = 5.6). Females in enclosures with grass changed direction more frequently (mean = 36.5 changes/h) than those in gravel enclosures (19.0 changes/h;  $P < 0.001$ ). In enclosures with gravel, high-ranking females changed direction significantly less frequently than low-ranking females ( $P = 0.002$ ) and also showed a tendency to change direction less frequently than mid-ranking females ( $P = 0.07$ ;  $N = 190$  females; Fig. 2). The linear prediction for

females in gravel was 10.7, 23.7 and 20.2 changes in direction/h for high-, mid- and low-ranking females, respectively, whereas the linear prediction for females in grass was 34.3, 31.8 and 40.8 changes in direction/h for high-, mid- and low-ranking females, respectively.

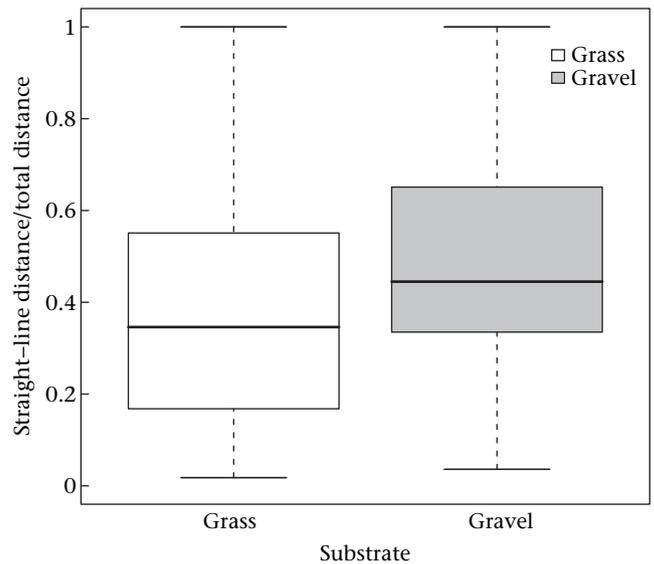
A gamma family regression model was fitted to total distance per hour ( $N = 147$ ). The best fit model included fixed effects for substrate, rank and the interaction term substrate  $\times$  rank, but this model differed only slightly from the second best fit model ( $\Delta$ AIC = 1.6), which had a single fixed effect for substrate. Thus, both models appeared equally good at explaining the observed variation in total distance. In the first model, substrate and the interaction term substrate  $\times$  mid-rank were significant (substrate:  $P = 0.02$ ; substrate  $\times$  mid-rank:  $P = 0.006$ ) and the interaction substrate  $\times$  low-rank approached significance ( $P = 0.07$ ; Fig. 3). The linear prediction of total distance travelled for females in gravel was 42.8, 82.7 and 64.9 m for high-, mid- and low-ranking females, respectively. The linear prediction of total distance for females in grass was 68.8, 67.3 and 68.0 m for high-, mid- and low-ranking females, respectively. In the second model, substrate was not a significant predictor of total distance travelled/h ( $P = 0.47$ ).

A gamma family regression model was fitted to the ratio of the straight-line distance to total distance travelled during a focal sample, referred to as the straightness index ( $N = 147$ ). The best fit model included a single fixed effect for substrate (compared to the second best model,  $\Delta$ AIC = 3.5). Animals in grass travelled significantly shorter straight-line distances relative to total distance than animals in gravel ( $P < 0.001$ ; Fig. 4). The linear prediction of the straightness index is 0.37 for grass substrate and 0.50 for gravel. Coefficients and standard errors of the best fit models for travel path characteristics are summarized in Table 3. Group size was included in the analyses of travel path characteristics, but was not a significant predictor of stops, changes in direction, or straightness index.

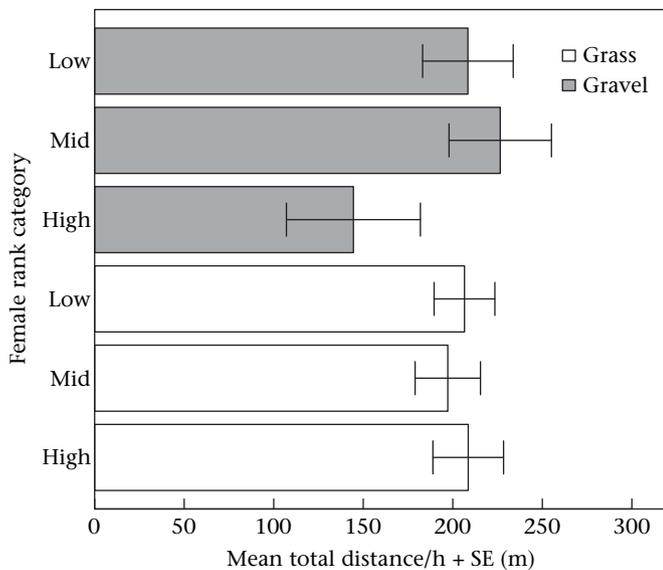
Group 2, which was moved from an enclosure with gravel to one with grass substrate halfway through the study, showed a similar pattern to the other six groups. When they were in the grass



**Figure 2.** Frequency of changes in direction per hour for rhesus macaques in each rank and substrate category. The number of times individuals changed direction/h for all sampled individuals' travel paths per rank category per substrate (grass:  $N = 38, 40, 48$  for high, mid and low rank; gravel:  $N = 18, 20, 26$  for high, mid and low rank). Boxes represent the interquartile range and the black bar is the median number of changes in direction/h. The upper (and lower) whiskers are drawn to the largest (or smallest) data point not lying above the 75th percentile (or below the 25th percentile) +  $1.5 \times$  IQR.



**Figure 3.** Straightness index for rhesus macaques in enclosures with grass or gravel substrate. The number of times individuals stopped/h for all sampled individuals' travel paths in grass ( $N = 126$ ) and gravel ( $N = 64$ ) substrates. Boxes represent the interquartile range and the black bar is the median straightness index. The upper (and lower) whiskers are drawn to the largest (or smallest) data point not lying above the 75th percentile (or below the 25th percentile) +  $1.5 \times$  IQR.



**Figure 4.** Mean + SE total distance/h for rhesus macaques in each rank and substrate category. The mean total distance travelled/h for all sampled individuals' travel paths per rank category per substrate (grass:  $N = 38, 40, 48$  for high, mid and low rank; gravel:  $N = 18, 20, 26$  for high, mid and low rank).

enclosure, animals in this group stopped more frequently than when they were in a gravel enclosure (Mann-Whitney  $U$  test:  $U = 189, N_1 = 15, N_2 = 17, P = 0.02$ ), and they changed direction more frequently when they were living on grass than on gravel ( $U = 210, N_1 = 15, N_2 = 17, P = 0.002$ ). They showed no significant difference in total distance ( $U = 127.5, N_1 = 15, N_2 = 17, P = 1.0$ ) or straightness index ( $U = 124, N_1 = 15, N_2 = 17, P = 0.9$ ). For all travel path characteristics (changes in direction, stops and straightness index), group size was not a significant predictor of travel path.

#### Movement Bouts

For movement bouts, the best fit model included fixed effects for substrate, apparent goal of the movement bout (feed or forage) and the interaction term substrate  $\times$  goal (compared to the second best model,  $\Delta AIC = 3$ ). In enclosures with grass substrate only, females travelled significantly shorter distances when the apparent goal was foraging for supplemental foods than when the apparent goal was feeding on monkey chow (apparent goal:  $P < 0.001$ ;

substrate  $\times$  goal:  $P = 0.008$ ;  $N = 812$  bouts; Table 4, Fig. 5). For grass substrate, the linear prediction of movement bout distance was 3.2 m for bouts prior to foraging on supplemental foods and 5.7 m for bouts prior to feeding on monkey chow. For gravel substrate, the linear prediction of movement bout distance was 5.2 and 6.0 m for bouts prior to foraging and feeding, respectively.

Movement bout speed varied by the apparent goal of the movement, but not by substrate. The best fit model included a fixed effect for apparent goal of the movement bout (compared with the second best model,  $\Delta AIC = 6$ ). Regardless of substrate, females travelled more slowly when the apparent goal was foraging for supplemental foods than when the apparent goal was feeding on monkey chow ( $P < 0.001$ ;  $N = 812$  bouts; Fig. 6). The linear prediction of movement bout speed prior to encountering supplemental foods was 0.53 and 0.62 m/s prior to feeding on monkey chow. Coefficients and standard errors of the best fit models for movement bout distance and speed are summarized in Table 5.

Animals in Group 2 showed a similar pattern. When Group 2 was in a grass enclosure, movement bouts whose apparent goal was foraging for supplemental foods were significantly slower ( $U = 74, N_1 = 7, N_2 = 11, P = 0.02$ ) and had a tendency to be shorter than bouts whose apparent goal was feeding on monkey chow ( $U = 68, N_1 = 7, N_2 = 11, P = 0.07$ ). In contrast, when members of Group 2 lived in a gravel enclosure, their movement bouts did not differ either by distance or speed when the apparent goal was different (bout distance:  $U = 62.5, N_1 = 8, N_2 = 10, P = 0.14$ ; bout speed:  $U = 40.5, N_1 = 8, N_2 = 10, P = 1.0$ ).

## DISCUSSION

### Value of Captive Studies for Movement Ecology

We found that movements of captive rhesus macaques were affected by the type of substrate in the enclosures. In enclosures with grass substrate, where supplemental food resources were denser and more randomly distributed, individuals stopped more frequently, changed directions more frequently and showed movement paths with smaller straightness indexes, indicating that movement paths were more tortuous in enclosures with grass substrate than they were in enclosures with gravel substrate. Despite the constraints on movements that captivity places on animals, our results are consistent with studies of movement patterns of wild animals. Movement paths of animals in the wild are more tortuous under random food distributions and higher food densities (McIntyre & Wiens 1999; de

**Table 3** Regression outputs of the best fit models for rhesus macaque travel path variables stops, direction changes, total distance and straightness index

Variable	Predictor	Estimate	SE	P
Stops	Substrate	-0.588	0.128	0.0001
	Mid rank	-0.037	0.091	0.69
	Low rank	0.091	0.092	0.32
	Substrate $\times$ mid	0.503	0.166	0.003
	Substrate $\times$ low	0.319	0.162	0.05
Change direction	Substrate	-1.166	0.203	0.0001
	Mid rank	-0.076	0.143	0.59
	Low rank	0.171	0.149	0.25
	Substrate $\times$ mid	0.827	0.263	0.002
	Substrate $\times$ low	0.465	0.259	0.07
Total distance	Substrate	0.0088	0.0036	0.02
	Mid rank	0.00033	0.0021	0.87
	Low rank	0.00017	0.0021	0.94
	Substrate $\times$ mid	-0.0116	0.0042	0.007
	Substrate $\times$ low	-0.0079	0.0043	0.07
Straightness index	Substrate	-0.681	0.204	0.001

**Table 4**

Means and standard errors of locomotion bout characteristics of rhesus macaques for bouts whose apparent goal was foraging or feeding

Group	Substrate	Feed distance (m)	Forage distance (m)	Feed speed (m/s)	Forage speed (m/s)
1	Grass	10.5±2.2	3.7±0.3	0.64±0.06	0.58±0.02
5	Grass	9.5±1.6	3.7±0.4	0.67±0.08	0.53±0.03
14	Grass	6.8±1.3	4.3±0.4	0.61±0.05	0.60±0.03
16	Grass	8.0±1.2	4.6±1.3	0.61±0.06	0.51±0.02
1, 5, 14, 16	Overall	8.9±0.8	4.1±0.4	0.63±0.03	0.56±0.01
8	Gravel	7.0±0.8	7.1±1.1	0.65±0.05	0.56±0.05
18	Gravel	7.9±1.2	7.6±1.2	0.69±0.05	0.54±0.05
8, 18	Overall	7.5±0.7	7.3±0.8	0.67±0.05	0.55±0.03
2	Grass	7.2±1.9	2.9±0.2	0.72±0.11	0.49±0.02
2	Gravel	8.2±1.5	5.7±1.1	0.61±0.09	0.62±0.08

The median values of movement bout characteristics for each individual were used to calculate the means and standard errors for movement whose apparent goal was either feeding on monkey chow or foraging for supplemental foods. Group 2 moved from a gravel enclosure to a grass enclosure 7 months into the study.

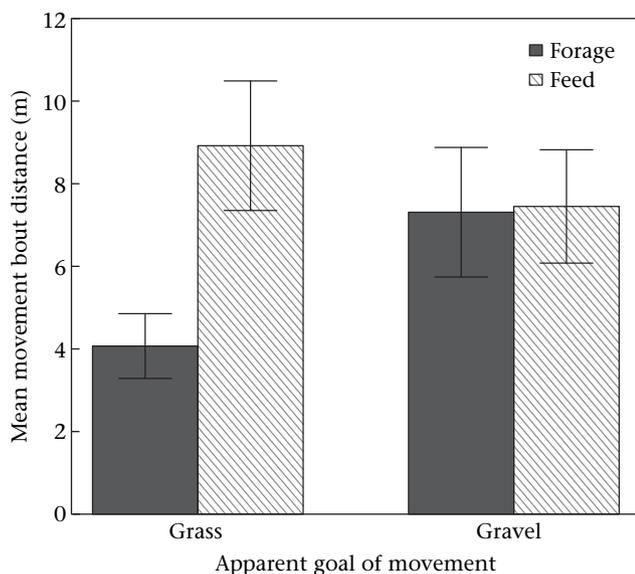
Knegt et al. 2007), or when searching for foods in unknown locations. Our study reveals the utility of monitoring the movements of animals in captivity to facilitate greater understanding of the factors underlying movement ecology, especially as the captive environment may be more amenable to manipulation of the distribution, density or predictability of food resources. This study augments previous work on both indoor and outdoor groups of captive macaques (Chamove et al. 1982; Byrne & Suomi 1991; Beisner & Isbell 2008; Jaman & Huffman 2008), which indicate that floor litters and ground substrate type have the capacity to influence macaque foraging patterns.

#### Ecological Factors Underlying Movement Paths

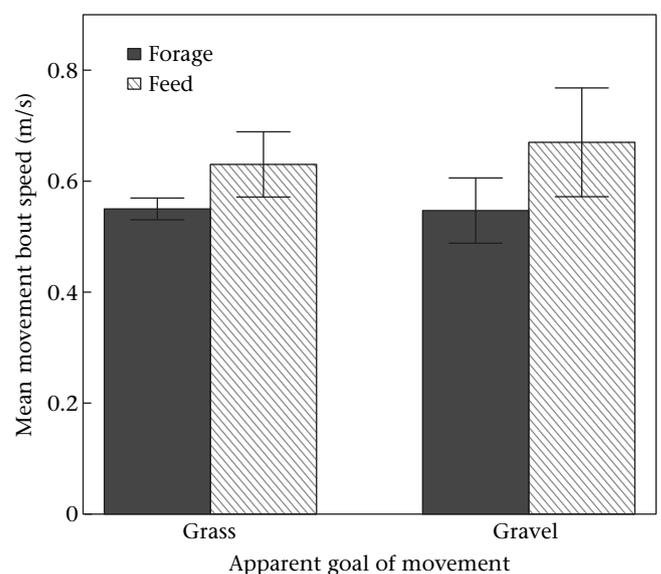
Travelling along a tortuous path may mean that our subjects were either less efficient in moving towards an apparent goal when in grass, or that they were moving along a random search path, searching for unpredictably located resources (Benhamou 2004). Whether they intended to forage more in grass (but did so inefficiently), or whether they foraged for unpredictable resources using a random search path is difficult to distinguish. However, the results suggest the latter interpretation. First, their more frequent stops in grass suggest that they encountered supplemental foods in

grass more frequently, and that the density of these foods was higher in grass than in gravel (Isbell et al. 1998). Indeed, high food density frequently elicits more tortuous paths among other animals (Crist et al. 1992; de Knegt et al. 2007), perhaps because the location of dense foods is not worth remembering. Shorter movement bouts prior to foraging for supplemental foods in grass substrate relative to gravel also suggest higher density of supplemental foods in grass. Second, their more frequent changes in direction in grass suggests that the location of supplemental foods was unpredictable for them. Finally, slower movement bouts whose apparent goal was foraging relative to bouts whose apparent goal was feeding on monkey chow suggests that the macaques did not know where the supplemental foods were located prior to encountering them (Pochron 2001; Noser & Byrne 2007).

What animals know about their foods also influences whether their foraging behaviour is purposeful or opportunistic. Predictably located foods can be remembered (Janmaat et al. 2006), and larger foods are more worth remembering than smaller, scattered foods (Terborgh 1983; Pochron 2001). Our subjects obviously knew the location of the monkey chow because it was always within sight. In contrast, food resources such as insects and grasses are so unpredictable or at such high density that remembering where they



**Figure 5.** Movement bout distance relative to the apparent goal for rhesus macaques in enclosures with grass or gravel substrate. Mean locomotion bout distance measured during locomotion bouts prior to feeding on monkey chow and prior to foraging for supplemental foods in enclosures with gravel ( $N = 30, 36$ ) and grass ( $N = 48, 84$ ) substrates. Error bars indicate 95% confidence intervals.



**Figure 6.** Movement bout speed relative to the apparent goal for rhesus macaques in enclosures with grass or gravel substrate. Mean locomotion bout speed measured for locomotion bouts prior to feeding on monkey chow and prior to foraging for supplemental foods in enclosures with gravel ( $N = 30, 36$ ) and grass ( $N = 48, 84$ ) substrates. Error bars indicate 95% confidence intervals.

**Table 5**  
Regression outputs for the best fit models for rhesus macaque movement bout speed and distance

Variable	Predictor	Estimate	SE	P
Bout distance	Apparent goal	−0.549	0.095	0.0001
	Substrate	0.055	0.144	0.77
	Goal×substrate	0.461	0.165	0.008
Bout speed	Apparent goal	−0.149	0.036	0.0001

occurred last is not useful knowledge (Janson 1996). The small size of the supplemental food items and quick movements of the monkeys made it difficult for the observer to consistently identify the type of food being eaten, suggesting that macaques also cannot visually detect these foods until within very close range (observer-identified food items included blades and roots of grass, arthropods and dirt). Visual detection of supplemental food items by macaques presumably varied by the height of the grass (grass enclosures only) and the contrast in shape and colour between the food items and the surrounding substrate. Macaques in grass had more tortuous paths than macaques in gravel, which suggests that grass enclosures encourage more opportunistic foraging behaviour.

#### *Social Factors and Movement Ecology*

Among animals with gravel substrate, social rank also influenced the tortuosity of travel. Lower-ranking animals changed directions and stopped more frequently than higher-ranking animals, suggesting that lower-ranking animals spend more time foraging for unpredictably distributed supplemental foods than do high-ranking animals. Furthermore, there was a tendency for low-ranking animals to have longer total distances than higher-ranking animals, which may also reflect a greater effort by lower-ranking animals to search for unpredictably located supplemental foods. We interpret these results as indicative of greater constraints on lower-ranking females arising from greater threat of aggression from higher-ranking females. Low-ranking females in this population have significantly greater hair loss than high-ranking females (Beisner & Isbell 2009), and hair loss is often a sign of social stress (Roloff et al. 1998; Steinmetz et al. 2006). Among wild populations, food competition sometimes results in lower-ranking animals travelling further to find food (Wittemyer et al. 2007), waiting their turn to feed on large, spatially clumped foods (Whitten 1983), or feeding on alternative, less preferred foods (Janson 1985).

The ability to use different movement strategies based upon the nature of food resources is likely to affect food competition among group members, whereby those individuals capable of greater behavioural flexibility or those under fewer social constraints may have better foraging efficiency and success. It has also been hypothesized that the degree to which animals are able to engage in tortuous movements as they go about obtaining their food may affect their success in dispersing or expanding their home ranges. Because dispersal, for instance, involves movement into new areas where the locations of food resources are unknown, tortuous movements are expected to increase as animals disperse, but if dispersers can energetically afford to make only direct movements between food sites, they may have difficulty surviving the dispersal phase (Isbell 2004). A greater understanding of how individuals move to encounter their food resources may also shed light on other aspects of animal behaviour, perhaps even the degree to which individuals group (Wrangham 2000; Isbell 2004).

In addition to the contribution of this study to theoretical issues, our results have more practical value. Movement and searching behaviour are primary occupations of wild animals, and captive enclosures clearly limit these behaviours, most obviously because

the dimensions of captive enclosures are usually quite small relative to wild home ranges. By providing supplemental foods that are unpredictably located, grass substrates increases the complexity of the environment and challenges the animals by encouraging opportunistic foraging behaviour. Among wild, free-ranging rhesus macaques, grasses sometimes constitute a large part of their diet (Goldstein & Richard 1989), and so providing grass substrate also gives captive macaques a food source they would normally eat in their natural habitat. In addition, grass substrate in outdoor enclosures reduces hair loss, reduces time spent grooming, increases time spent foraging, and may reduce the stress that appears to be associated with low rank (Beisner & Isbell 2008, 2009). The present study reveals that grass substrate can also significantly influence animal movement and is further indication that even simple changes in the captive environment can have large effects on behaviour and well-being (Dawkins 1983; Karlen et al. 2007).

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