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# Movement characteristics of American beavers (*Castor canadensis*)

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## Abstract

Physiological states and foraging behaviors may shape movement patterns of animals. Optimal foraging theory and what we term the deliberate movement hypothesis predict that, to reduce predation risk, central place foragers should move faster with smaller turning angles the further they are from their central place. The complementary bimodal foraging trip hypothesis predicts that the distribution of foraging distances exhibited by central place foragers should be bimodal due to a trade-off between provisioning offspring and self-feeding. We used radio-telemetry to test these hypotheses for American beavers (*Castor canadensis*) in northern Alabama, United States. American beavers moved faster with increasing distance from lodges in wetland land cover but not in terrestrial land covers, partially supporting the deliberate movement hypothesis. Hourly distances moved from lodges were distributed bimodally during the breeding season, which supports the bimodal foraging trip hypothesis. Therefore, central place foraging may be a determinant of movement characteristics of American beavers.

## Keywords

bimodal foraging distance, central place foraging, movement distance, optimal foraging.

## 1. Introduction

Movement ecology has recently re-emerged as a central theme of animal ecology although animal movements have been one of the oldest study topics (Pulido, 2007; Nathan, 2008). Animals move to search for and acquire

resources and mates as well as to escape predators. Animals may adjust the distances and directions (i.e., turning angles) of their movements based on temporal and spatial variation in resource availability and predation risk (Getz & Saltz, 2008; Mueller & Fagan, 2008; Nathan et al., 2008). Movement distances and turning angles may also be related to physiological and behavioral (e.g., foraging, resting and travelling) states of moving animals (Franke et al., 2004). Behavioral states and patterns (such as central-place foraging and patrolling foraging) may constrain movement characteristics (e.g., speed and turning angle) of animals and their responses to spatiotemporal variation in resource availabilities (Getz & Saltz, 2008; Mueller & Fagan, 2008; Nathan et al., 2008). However, few studies have investigated relationships between behavioral patterns and movement ecology of semi-aquatic mammals (Di Stefano et al., 2011; Campbell et al., 2013).

Patterns of foraging behavior may have profound consequences on patterns of movement and use of space by animals (Owen-Smith et al., 2010; Buchmann et al., 2012). Central place foraging theory states that food searching and handling time, travel time between patches of resources, and energetic costs of resource acquisition influence foraging decisions of central place foragers (Orians & Pearson, 1979; Fryxell, 1992). To maximize energetic returns, central place foragers may reduce foraging time but increase food item size with increasing distance from their central places such as dens, nests, or lodges (Fryxell, 1992). Predation risk can also influence foraging distance (Andersson, 1978; Getty, 1981). Thus, tradeoffs between maximizing energetic return and minimizing predation risk may lead to an inverse relationship between foraging time per unit area and distance travelled from the central place (Fryxell, 1992). What we term the deliberate movement hypothesis predicts that central place foragers should move more deliberately (i.e., at higher speed with smaller turning angles) the further they are from their central place to reduce risk of predation. To our knowledge, no studies have tested the deliberate movement hypothesis using fine-scale movement data.

Patterns of parental care and the need to provision offspring can also influence movement patterns of central place foragers. Foraging distances of nesting seabirds are often bimodally distributed because individuals alternate between short, frequent foraging trips to provision young with long foraging trips to obtain food for themselves (i.e., the bimodal foraging trip hypothesis; Weimerskirch et al., 1994; Ropert-Coudert et al., 2004; Ludynia et al.,

2013). Central place foragers may spend less time foraging on long trips than on short trips because of predation risk (Fryxell, 1992). Ydenberg & Davies (2010) predicted that bimodal foraging trips are widespread among central place foragers. However, although this hypothesis has been tested repeatedly for seabirds, few studies have tested whether foraging distances of individuals are bimodally distributed for mammals (Fryxell & Doucet, 1991; Fryxell, 1992).

Intrinsic factors, such as physiological states and ages, and extrinsic factors, such as seasonality and resource availability, may also affect animal movements, partially by affecting foraging and movement decisions. Patterns of animal movement may vary between age groups due to differences in dispersal propensity and reproductive activity (Mueller & Fagan, 2008; Owen-Smith et al., 2010). For instance, mammal dispersal is often skewed to juveniles, and juveniles may make exploratory movements before natal dispersal for reproduction (Greenwood, 1980; Wolff, 1993; Selonen & Hanski, 2006; Debeffe et al., 2013). Animals may also increase movements and enlarge home ranges from spring and summer to winter as local food availability declines (Schradin et al., 2010). Therefore, movement distances and home-range sizes may differ between age groups and seasons.

American beavers (*Castor canadensis*, hereafter beavers) are semi-aquatic herbivores that build bank dens or lodges for shelter and nursing of young (Collen & Gibson, 2000). Beavers are central place foragers who make foraging trips from a lodge or bank den (hereafter lodge) to a forage patch and back, in order to avoid predators, consume food, and care for young at the lodge (Jenkins, 1980; Fryxell, 1992). Beavers are socially monogamous and live in social groups; consequently, adults and philopatric yearlings may spend more time at or near lodges during the breeding season to nurse and protect young than at locations further from the lodge (Baker & Hill, 2003). Like nesting sea birds, beavers may exhibit bimodal foraging trips during the breeding season, with a mode of short foraging trips near the lodge for nursing and protecting newborns and a mode of long foraging trips for self-feeding to acquire sufficient amounts of food. Therefore, the American beaver represents a useful model species for evaluating the effects of central place foraging on movement patterns of mammals.

Previous studies of central place foraging by beavers have focused on relationships between distance from lodges (Fryxell, 1992) or from shorelines (Jenkins, 1980) and selection of food items based on size (Brzyski & Schulte,

2009). However, few studies have investigated fine-scale movement characteristics of beavers in the context of central place foraging theory. In this study, we tested two hypotheses about foraging behavior in beavers. First, we tested the deliberate movement hypothesis which predicts that, to reduce predation risk, beavers should move faster with smaller turning angles the further they are from their central place (i.e., lodge). Second, we tested the bimodal foraging trip hypothesis which predicts that movement distances of adult and subadult beavers from their lodges should be distributed bimodally with frequent short trips for provisioning offspring combined with longer distance movements for self-feeding. Dispersal of beavers is skewed toward subadults (2 years old; Allen, 1983; Collen & Gibson, 2000) and subadults may make exploratory movements to sample settlement habitat before dispersal (Havens, 2006). Therefore, we also tested the hypothesis that annual home ranges and distances moved from lodges by subadult beavers would be greater than those of adults ( $\geq 3$  years old) and yearlings (1 year old).

## **2. Material and methods**

### *2.1. Study area*

We conducted the study at Redstone Arsenal (RSA), a 15 342-ha Department of Defense military installment located in Madison County, AL, USA (34°38'N, 86°39'W). The arsenal is bordered by the cities of Huntsville to the north and east and Madison to the west, with the Tennessee River as the southern boundary. Average monthly temperatures ranged from 8°C in December 2012 to 28°C in July 2011, with an average monthly temperature of 18°C throughout the study. Total precipitation from May 2011 to April 2012 was 125.5 cm, and monthly precipitation varied from 3.4 cm in October to 19.8 cm in January (Huntsville-Decatur International Airport weather station, the National Oceanic and Atmospheric Administration station ID: 014064; approximately 14 km from our study sites). The RSA landscape was relatively flat with elevation ranging from 165 to 365 m. The landscape was composed of agricultural fields, military test ranges, upland pine forests, mixed forests, and different types and quality of beaver habitat, such as bottomland hardwood forests, various water bodies, and many seasonal swamps and marshes that became inundated with water during the rainy season. We used the National Land Cover Classification Database 2006 (available online at <http://www.mrlc.gov/nlcd2006.php>) to derive a land cover and land

use map at the 30-m resolution for the study area (Fry et al., 2011). The original four levels of developed class (classes 21–24) were combined into one class (i.e., developed area). The resulting land cover types included water, developed area, deciduous forest, evergreen forest, mixed forest, shrubland, grassland, cropland and wetland (Figure 1).

We studied beavers from 11 wetlands located predominantly in the southern half of RSA. The 11 wetlands varied in size, shape, and type and were initially selected due to presence of beaver activity. Average distance between sites was 4942 m, with a minimum distance of 278 m and maximum distance of 9806 m.

## 2.2. Capture, tagging and radio telemetry

From 21 January to 11 May 2011, we live captured beavers using Hancock live traps, which weigh 15 kg and have dimensions of 71 × 91 × 10 cm (Hancock Trap, Custer, SD, USA). We placed Hancock traps next to dams, movement corridors and scent mounds of beavers in each of the 11 wetlands. Commercial castor or food-based lures (Backbreaker or Woodchipper, Dobbins' Products, Goldsboro, NC, USA) were used to attract beavers and increase trapping success. We activated traps with lures daily before 15:00 h and checked traps the following morning by 09:00 h.

We weighed captured beavers to the nearest 0.1 kg in their traps using a hanging scale (Moultrie Feeders, Alabaster, AL, USA). We classified captured beavers into four age classes according to body mass following Breck et al. (2001): <6.8 kg as 0–12 month old kits; 6.8–10.8 kg as 13–24 month old yearlings; 10.9–16.0 kg as 25–36 month old subadults; and >16 kg as ≥37 month old adults.

We anesthetized beavers weighing >6.8 kg with an intramuscular injection of ketamine hydrochloride (10 mg/kg) and xylazine hydrochloride (1 mg/kg) before radio tagging live beavers (Havens, 2006; Arjo et al., 2008; Bloomquist & Nielsen, 2010). We then attached radio transmitters (Model 3530, ATS, Isanti, MN, USA), weighing <0.05% of beaver body mass, to tails of anesthetized beavers using methods first developed by Rothmeyer et al. (2002) and modified by Arjo et al. (2008). Transmitters had an estimated battery lifetime of 647 days. We monitored body temperatures, pulses, and respiration rates of anesthetized beavers during radio transmitter attachment.

After secure transmitter attachment, we inserted a passive integrated transponder (PIT tag; Avid Identification Systems, Norco, CA, USA) subcutaneously between the scapulae with a single use disposable syringe for

permanent identification of beavers (Bond et al., 2001; Arjo et al., 2007). We released radio-tagged beavers at the location of capture once fully recovered (i.e., alert and responsive). Sedation and handling time ranged from 30–60 min/beaver. Trapping and handling of beavers was approved by the Institutional Animal Care and Use Committee of the United States Department of Agriculture, National Wildlife Research Center (Protocol No. QA-1626).

We monitored beaver movements throughout a 12-h period (18:00–06:00 h) on foot using an ATS hand-held 3-element Yagi antenna, an R-1000 receiver (Communications Specialist, Orange, CA, USA) and a look-through compass (Model KB-20/360R, Suunto, Vantaa, Finland). We modified the compass for nighttime radio telemetry using a clear straw and 3.81-cm miniature glowing sticks. We located radio-tagged beavers using triangulation methods with at least three position fixes per location by taking  $\geq 3$  azimuths with an overall separation of 60–120° in  $\leq 15$  min (Cochran et al., 1963; White & Garrott, 1990). We recorded Universal Transverse Mercator (UTM) coordinates of observer positions using a handheld Global Positioning System (GPS) unit (Model GPSMap 76, Garmin, Olathe, KS, USA) with  $\leq 3$  m accuracy. Approximately 3° were subtracted from each azimuth before estimating beaver locations to account for compass declination throughout the study period (available online at <http://www.ngdc.noaa.gov/geomagmodels/struts/calcDeclination>). We estimated UTM coordinates of radio-tagged beavers using program LOCATE III (Nams, 2006).

### 2.3. *Hourly movement distances*

We monitored hourly movements of beavers at Igloo Pond and Igloo Drain, approximately 1030 m apart (Figure 1), by locating all beavers in the two wetlands hourly throughout a 12-h period (18:00–06:00 h) via triangulation methods. We repeated hourly monitoring 12 times from 17 May 2011 to 29 June 2011 in 2–5-day intervals for the dry season and once on 13 March 2012 for the wet season. Dry season at our study site was from April through August with seasonal total precipitation of 37.95 cm, and wet season was from September through March with seasonal total precipitation of 87.60 cm. We calculated Euclidian distance (m) between two successive locations and relative turning angles ( $\theta$ ) using function `as.ltraj` in R package `adehabitatLT` (Calenge, 2006), as well as distance from the departing location of an hourly trip to lodge (in m) using function `spDistsN1` in R package `sp` (available online at <http://rspatial.r-forge.r-project.org>) in the R

2.13.1 environment (R Development Core Team, 2011). We identified lodges by searching for radio-tagged beavers during the middle of daylight hours. We calculated average hourly distance moved, average relative turning angle, and average hourly distance from the main lodge by season for all radio-tracked beavers. Hourly distances moved by beavers were used to model the distribution of foraging trip distance. Locations were collected hourly so distances moved between two consecutive locations were converted to hourly movement speed (m/h).

#### 2.4. Home range, core use area and distance moved from lodge

We monitored radio-tagged beavers at least two times per week from 9 May 2011 to 27 July 2011 and bi-weekly from 19 August 2011 to 20 April 2012. We systematically varied the order in which we tracked beavers in each wetland and the time of night of radio tracking for each beaver across all tracking occasions to ensure that the temporal distribution of estimated locations was unbiased over the beavers' most active periods between 17:00 and 08:00 h (Mott et al., 2011). We only considered beavers having  $\geq 20$  locations with location estimates of 95% error ellipse  $< 0.5$  ha throughout the study period for annual home-range estimation ( $N = 26$  beavers). We estimated annual home-range size (ha) for each radio-tagged beaver using the kernel density estimation (KDE) method with a least squares cross validation smoothing parameter (Worton, 1989). We estimated 50% and 95% KDE using ArcMap10 (ESRI, Redlands, CA, USA) through the Geospatial Modelling Environment (GME version 0.7.1.0, Toronto, ON, Canada) and the R 2.13.1 environment. We used 50% KDE home ranges as core use areas of radio-tagged beavers. In a preliminary analysis, we found that three beavers at Thiokol Wetland had home-range sizes 5–8-times larger than those of the remaining 23 beavers. Therefore, we calculated mean home-range sizes based on all 26 individuals as well as after excluding these three individuals from Thiokol Wetland.

We calculated mean distance and maximum distance moved from each individual's lodge (m) by season using function `spDistsN1` in the R package `sp`. We then calculated seasonal mean distance and mean maximum distance to lodges of beavers by age class and season.

#### 2.5. Statistical analysis

We conducted linear regression to evaluate relationships between distance of departing location from lodge and hourly movement speed during the dry

and wet season, using generalized linear models in the SAS procedure GLM (SAS, version 9.2, SAS Institute, Cary, NC, USA). We excluded data points from the regression where distance to lodge values were equal to hourly moving speed values. In a preliminary analysis, the slope of the regression including all hourly movement data indicated a similar relationship as the one obtained from the subset of data. Thus, exclusion of the data points did not change the relationship pattern between distance of departing location from lodge and hourly movement speed. We calculated correlation between relative turning angle and distance from lodge using circular linear correlation (Batschelet, 1981). Mean and standard deviation of relative turning angles were computed with the R package *circular* (available online at <https://r-forge.r-project.org/projects/circular/>).

We used the expectation-maximization method in the R package *mixtools* (Benaglia et al., 2009) to fit three different finite mixture models to data on distance from lodge for the dry and wet seasons to determine if beaver movements away from the lodge fit a unimodal or bimodal movement distribution. The three models included a mixture of two normal distributions with different means and different variances, a mixture of two normal distributions with different means and identical variances, and a single normal distribution. We used the Akaike information criterion (Burnham & Anderson, 2002) to select the best approximating model with the lowest AIC value and competing models with a  $\Delta\text{AIC} < 2$  for each season (Burnham & Anderson, 2002). The  $\Delta\text{AIC}$  of a model is the difference in AIC between the model and best approximating model.

We used mixed-effects analysis of variance (ANOVA) in the SAS procedure MIXED with the Tukey–Kramer adjustment to compare mean home-range sizes and mean distances moved from the lodge between age groups with individual beaver identification number (ID) as a random factor nested within wetland ID to account for interdependence of movements between beavers in the same wetland. We used natural logarithmic transformation to normalize home-range data (Di Stefano et al., 2011; Bloomquist et al., 2012). All tests were conducted at  $\alpha = 0.05$  and all means were reported  $\pm 1$  SD.

### **3. Results**

We captured 50 beavers from 11 wetlands (Table 1). Twenty-four beavers were not included in analyses due to transmitter loss or failure. We monitored 26 beavers at nine wetlands for 12 months (Figure 1).

**Table 1.**

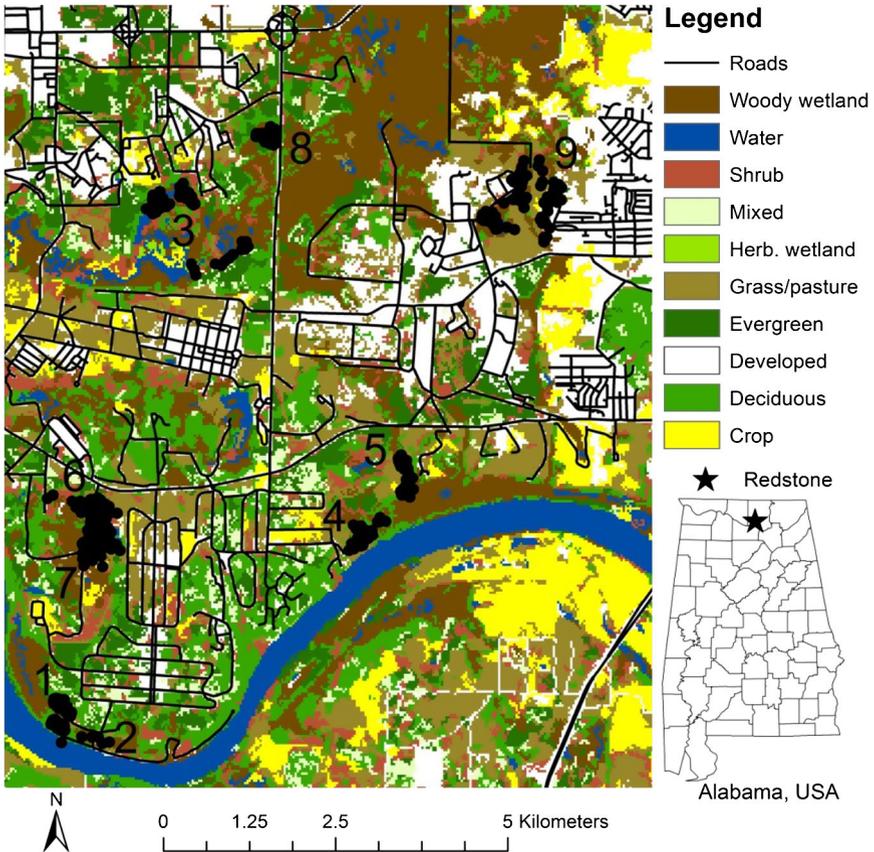
Captures by age group of American beavers in Redstone Arsenal, Madison County, AL, USA.

Wetland name	Total capture	Adult	Subadult	Yearling
Blueberry	5	2(0)*	2(0)	1(0)
Corkwood Road	1	0	1(1)	0
Corkwood	4	2(2)	0	2(2)
DDT Abatement	6	2(0)	2(1)	2(1)
DDT Spring Branch	6	4(0)	2(0)	0
Hudson Park Field	8	3(0)	5(2)	0
Hudson Park	2	1(1)	1(1)	0
Igloo Drain	4	2(1)	2(2)	0
Igloo Pond	8	5(4)	2(2)	1(1)
Patton Road	3	2(1)	0	1(1)
Thiokol Pond	3	3(3)	0	0
Total	50	26(12)	17(9)	7(5)

\* Numbers in parentheses are the numbers of animal radio tracked during the study period.

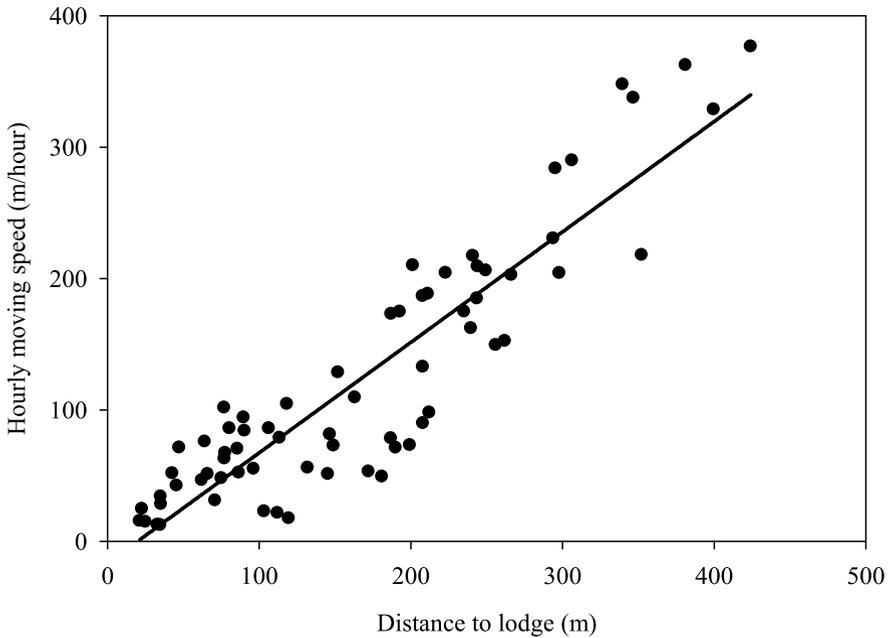
We calculated mean hourly movement distances for seven beavers from the Igloo Pond (IPW) colony and three beavers from the Igloo Drain (IDW) colony during the dry season of 2011 and five for IPW and three beavers for IDW during the wet season of 2012. Mean hourly movement distances were  $138.44 \pm 86.37$  m during the dry season and  $126.93 \pm 119.97$  m during the wet season for IPW, whereas mean hourly movement distances were  $90.95 \pm 58.29$  m during the dry season and  $124.68 \pm 91.55$  m during the wet season for IDW. Mean hourly turning angles were  $-3.06 \pm 1.33$  during the dry season and  $-2.77 \pm 2.30$  during the wet season for IPW; meanwhile, mean hourly turning angles were  $-3.00 \pm 1.47$  for the dry season and  $-2.96 \pm 1.39$  for the wet season for IDW.

Hourly moving speed of beavers was not related to distance from the main lodge for beavers in IDW ( $R^2 = 0.001$ ,  $F_{1,406} = 0.45$ ,  $p = 0.505$ ). In IPW, the  $p$  value was  $<0.05$ ; however, the  $R^2$  of the linear model for IPW was  $<0.1$  ( $R^2 = 0.02$ ,  $F_{1,413} = 9.54$ ,  $p = 0.002$ ). Thus, we concluded that hourly moving speed of beavers was not related to distance from the main lodge for beavers in IPW. Relative turning angles were not correlated with distance from the lodge during the 2011 dry season ( $\rho = 0.11$ ,  $p = 0.05$ ), but were correlated with distance from the lodge during the 2012 wet season ( $\rho = 0.42$ ,  $p = 0.03$ ). Likewise, relative turning angles were not related to



**Figure 1.** Landcover map and locations of nine wetlands where American beavers were radio tracked. Dots on the map represent telemetry relocations of beavers. Numbers on the map are indices for wetlands: (1) Corkwood Road, (2) Corkwood, (3) DDT Abatement, (4) Hudson Park, (5) Hudson Park Field, (6) Igloo Pond, (7) Igloo Drain, (8) Patton Road and (9) Thiokol Pond. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1568539x>.

distance from lodge on wetland land cover, with the 2011 and 2012 data combined ( $\rho = 0.1$ ,  $p = 0.36$ ). However, hourly moving speed was related positively to distance from the lodge for the subset of beaver locations in wetland areas ( $R^2 = 0.83$ , slope = 0.84,  $t = 17.68$ ,  $df = 67$ ,  $p < 0.001$ ; Figure 2). The best model for the distribution of hourly movement distances from the lodge was a bimodal-distribution model for the 2011 dry and 2012 wet seasons (Table 2 and Figure 3).



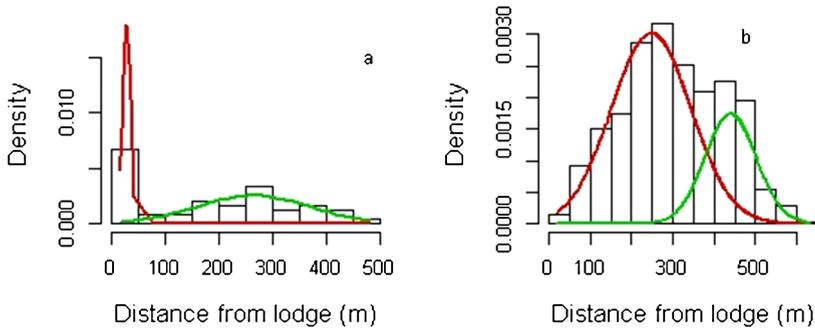
**Figure 2.** Relationship between distance from main lodge and hourly step distance of American beavers in wetland land cover at Igloo Pond and Igloo Drain Wetlands, Madison County, AL, USA, May 2011–June 2011 and March 2012.

Mean annual 95% KDE home-range sizes were  $20.89 \pm 26.54$  ha for 26 beavers but  $11.86 \pm 5.66$  ha for 23 beavers when excluding three Thiokol Wetland beavers with unusually large home ranges. Mean annual 50% KDE core use areas were  $4.55 \pm 6.87$  ha for 26 beavers but  $2.20 \pm 1.17$  ha for the

**Table 2.**

Model selection for the distributions of hourly movement distances from the lodges of American beavers at Igloo Pond and Drain Wetlands, Madison County, AL, USA, from May to June of 2011 and in March 2012.

Model	May–June 2011	March 2012
Mixture of two normal distributions with different means and variances	12 020.17	564.88
Mixture of two normal distributions with different means and same variance	12 056.91	617.05
Single normal distribution	12 054.91	615.03



**Figure 3.** Estimated density functions for distributions of hourly distances from lodges of American beavers at Igloo Pond and Igloo Drain Wetlands, Madison County, AL, USA during (a) March 2012 and (b) May–June 2011. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1568539x>.

23 beavers. There was no difference in mean annual 95% KDE home-range sizes or mean annual core use areas between age classes in the analysis of 26 radio-tagged beavers ( $p > 0.05$ ). After excluding three beavers with unusually large home-ranges from Thiokol wetland from the analysis, 50% KDE home ranges or core areas of subadults were larger than those of yearlings ( $t = 2.98$ ,  $df = 13$ , adjusted  $p = 0.027$ ). Neither age class nor season was significant in a mixed ANOVA of mean and maximum distances from the main lodge ( $p > 0.05$ ).

#### 4. Discussion

As predicted by the deliberate movement hypothesis, we found that beavers moved faster with increasing distance from their lodge in wetlands, probably to avoid predation risk (Figure 2). However, radio-tagged beavers did not appear to move faster in upland areas when further away from their lodges. The distribution of hourly distance from lodges was bimodal (Figure 3), consistent with the prediction of the bimodal foraging trip hypothesis for central place foragers (Weimerskirch et al., 1994). Furthermore, subadult beavers had larger core use areas than yearlings, possibly due to pre-dispersal exploratory movements.

Predation risk is a selective pressure on movement patterns of animals, including central place foragers (Boyce, 1981; Fryxell, 1992). Beavers may spend less time foraging as they move farther away from a central place to

reduce risk of predation risk (Jenkins, 1980; Novak, 1987; Fryxell, 1992) and Boyce (1981) suggested that beavers forage close to the shoreline to reduce predation risk. However, we found no evidence that beavers moved faster with increasing distance from their lodges when travelling in upland habitat. Multiple factors may contribute to the lack of evidence supporting the deliberate movement hypothesis in upland areas. First, beavers are known to construct multiple bank dens and lodges throughout their home range (Baker & Hill, 2003). Covich (1976) suggested that a multiple refuge strategy may allow burrowing herbivores access to more foraging areas with a decreased risk of predation. Beavers might have used different locations throughout the upland area of Igloo Wetlands as refuges, and this condition may have prevented us from detecting the predicted relationships between movement speed or relative turning angle and distance from the main lodge. Second, beavers may have few effective terrestrial predators in the southeastern United States (Bloomquist & Nielsen, 2010) and, therefore, be less wary of terrestrial predation compared to smaller, more vulnerable central place foragers. Common mammalian predators found in the southeastern US, such as bobcats (*Lynx rufus*), coyotes (*Canis latrans*) and river otters (*Lontra canadensis*), contribute little to the predation of beavers (reviewed by Baker & Hill, 2003). Alligators (*Alligator mississippiensis*) may also feed on beavers (Hill, 1976; Novak, 1987). Although we did not detect any sign of alligators at wetlands where we radio tracked beavers, predation by alligators might act as selective pressure on beavers in the southeastern US. Aquatic predation as a selective pressure may explain the inverse relationship between movement speed and distance from the lodges in wetlands (Figure 1).

We found support for the bimodal foraging trip hypothesis for beavers, with a bimodal distribution of hourly movement distance during the breeding seasons (Figure 3). Radio-tagged beavers spend more time at or near lodges to nurse and protect newborns in May-June, when birth or parturition peaks, than in March, when parturition just begins (Collen & Gibson, 2000). The bimodal foraging trips may result from the tradeoff between provisioning young and self-feeding by adults (Weimerskirch et al., 1994; Ropert-Coudert et al., 2004), particularly when self-feeding locations differ from locations where provisioning occurs (Ydenberg & Davies, 2010). Future studies are warranted to measure the duration of feeding trips and locate feeding habitat to test the bimodal foraging hypothesis in American beavers.

Our results also support the hypothesis that subadult beavers have stronger movement propensity than yearlings as core home-range areas and 50% home KDE home ranges of subadults were larger than those of yearlings. McNew & Woolf (2005) found that proportions of dispersing subadult beavers (2 years old) were greater than those of yearling beavers in Illinois. Pre- and post-dispersal exploratory movements within home ranges may increase the core use areas of subadult beavers, as seen with flying squirrels (*Pteromys volans*) (Selonen & Hanski, 2006). In summary, beavers moved faster in wetland habitat (probably in water) as distance from their main lodge increased, which is consistent with potential high predation risk by aquatic predators such as alligators in our site. The apparent lack of deliberate movements in uplands was likely due to either existence of multiple refuges within beaver home ranges and low predation risk by terrestrial predators in the southeastern US. Beavers appeared to make bimodal foraging trips during the breeding season probably due to tradeoffs between travelling farther to feed themselves and staying close to lodges to nurse and protect newborns. Taken together, our results support the overarching hypothesis that patterns of foraging behavior and age-related physiological states shape the movement ecology of beavers in our study system. Future studies of relationships between the movement patterns of American beavers and predation risks in different contexts of habitat, such as upland and wetland habitats, are needed for better understanding of the movement ecology of American beavers and other semi-aquatic mammals.

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