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Ecological and phenotypic effects on survival and habitat transitions of white-footed mice

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Animals often confine their movements to familiar areas and preferred habitats, resulting in increased fitness through enhanced survival and reproduction. However, the link between preferential habitat use and fitness is rarely tested, especially when individual phenotype is considered. Through multi-state modeling of mark-recapture data, we assessed the influence of habitat type, sex, and body size on the daily survival and habitat-transition probabilities of white-footed mice (*Peromyscus leucopus*). Habitat states tested were forest edge versus forest interior, and grassy versus shrubby habitat. Females were more likely to survive than males, and mass had a positive effect, whereas foot length a negative effect on survival. Females were more likely to exhibit habitat-type fidelity between edge and interior states than males. Body mass negatively affected daily transition between edge and interior, whereas foot length had a positive effect. Individuals were most likely to remain within the shrubby habitat and leave the grassy habitat. Mass had a negative effect on daily transition probability between grassy and shrubby habitats, foot length had a positive effect, and sex had no effect. Individuals with the greatest probability of moving between habitat types had the lowest probability of survival, likely a result of occupying unfamiliar space. Our results show that white-footed mice in general seem to select habitat types where fitness expectations are likely to be greatest, but that transitions between habitats often depend on phenotypic characteristics of individuals.

Key words: fitness, habitat type, mark-recapture, multi-state model, *Peromyscus leucopus*, space familiarity

Animal movement during habitat choice is a fundamental process that greatly affects patterns of ecology and evolution, influencing the distribution and abundance of organisms within and among populations, communities, and ecosystems (Holyoak et al. 2008; Nathan et al. 2008; Patterson et al. 2008; Cagnacci et al. 2010). Most animals confine their activity to areas with which they are relatively familiar (Piper 2011; Berner and Thibert-Plante 2015; Bevanda et al. 2015). The development of such preferential habitat use may offer direct fitness benefits in the form of elevated survival. Tests demonstrating a link between habitat preference, the likelihood of moving between habitats, and survival are rare, however (Garshelis 2000; Hoogland et al. 2006; Brown et al. 2008). Furthermore, relatively few studies have addressed how an individual's phenotypic characteristics, such as sex or body size, affect habitat transitions and the related fitness consequences (Holyoak et al. 2008; Delaney and Warner 2016).

The widespread abundance and generalist nature of the white-footed mouse (*Peromyscus leucopus*), which can be found across eastern North America and occupies a variety of habitat types, including woodland, grassland, and agricultural fields (Lackey 1978; Cummings and Vessey 1994; Nupp and Swihart 2000), has permitted several studies of differential habitat use and movement patterns (M'Closkey and Fieldwick 1975; Dueser and Hallett 1980; Richardson 2010). Few studies, however, have examined how habitat use varies with both sex and body size (Seagle 1985; Halama and Dueser 1994; Dooley and Bowers 1996; Klein and Cameron 2012), and fewer still incorporated a measurement of actual transitions between habitats rather than abundance patterns to explore differences (Klein and Cameron 2012). The survival consequences of preferential habitat use by white-footed mice have been understudied, especially within sex and body-size categories.

Peromyscus leucopus preferentially uses structurally complex habitats, such as those with extensive vertical structure, dense undergrowth, and large trees and logs (Myton 1974; Barry and Francq 1980; Kaufman et al. 1983; Barnum et al. 1992). Edge habitats and areas with more shrubby growth can

have more vertical structure and higher plant species diversity (Wiens 1974; Edwards 1983; Oosterhoorn and Kappelle 2000). Mice thus should be more likely to move toward forest edge or shrubby habitat and less likely toward habitats that are within the forest interior or more grassy. Individual dispersal between habitats, which can be influenced by population density, aggression, and the presence of nearby conspecifics of the opposite sex (Metzgar 1971; Hansen and Batzli 1978; Krohne et al. 1984), is typically biased toward males and juveniles (Krohne et al. 1984; Wolff and Lundy 1985). When density and aggression affect dispersal, the small-bodied, subordinate individuals are those that tend to disperse (Metzgar 1971; Hansen and Batzli 1978; Van Horne 1982; Halama and Dueser 1994).

Using mark-recapture data collected across a single season, and a multi-state modeling approach, we investigate how movement patterns in white-footed mice relate to fitness using daily survival estimates. Because structurally complex habitats are thought to be preferred, and preferred habitats may confer a survival advantage (Barnum et al. 1992; Garshelis 2000), we predicted that mice are more likely to stay within the forest edge and in shrubby habitats where they have higher survival. Because movement between habitats is risky (Hoogland et al. 2006; Clobert et al. 2012) and males, juveniles, and subordinates are more likely to move, we predicted that males and smaller-bodied individuals would have reduced survival.

Materials and Methods

Study site.—The study was conducted at the Mary K. Oxley Nature Center (−95.903°N, 36.223°E), located approximately 11 km northeast of downtown Tulsa, Tulsa County, Oklahoma, United States. The study site covers both forest and maintained prairie habitat (Fig. 1). The former is dominated by oak (*Quercus macrocarpa* and *Q. palustris*), cottonwood (*Populus* spp.), elm (*Ulmus* spp.), and green ash (*Fraxinus pennsylvanica*), whereas the prairie mainly consists of Johnson grass

Fig. 1.—Map depicting the portion of the Mary K. Oxley Nature Center in Tulsa, Oklahoma, where the mark-recapture study was conducted during 2015. Grid-based trapping sites are shown by symbols that also indicate the habitat type at each forest trap site.

(*Sorghum halepense*), big bluestem (*Andropogon gerardii*), and indiangrass (*Sorghastrum nutans*). Fallen trees and exposed roots are numerous throughout the forest habitat.

Sample collection.—We conducted a mark-recapture study in a forest habitat from March through December 2015. During the first 3 months, due to inclement weather, trapping was conducted irregularly in multiple 300-m transects across the study site until a feasible trap-grid area was determined. The prairie divided the forest and created a prominent forest edge (Fig. 1); however, no white-footed mice were ever captured in the prairie (despite our placing 56 traps in a 7 × 8 grid in the prairie and operating them with the same frequency as in the forest—Hannebaum 2016). Starting in June, Sherman SFA (H. B. Sherman Traps, Inc., Tallahassee, Florida) live traps were placed in the forest in 2 grids of 48 traps with 20-m spacing between each trap (Fig. 1). Within each trap, hay and oats were provided and replaced as required. Trapping sessions were conducted over 4 consecutive nights, weather permitting, with traps set in the evening, checked, and then closed every morning. Trapping sessions lasted 4 nights and occurred every 3 weeks to avoid biasing movement patterns of "trap-happy" mice. All trapping sites within the grid were GPS marked using a handheld Garmin Oregon 450t (Garmin Ltd., Olathe, Kansas) for spatial analysis and to ensure traps were positioned at the same location every session. Upon initial capture, individual mass, sex, right hind foot length, and location of capture were recorded, and an individual ID number was assigned. Using GPS coordinates for each trapping site, we determined the maximum distance moved (m) between traps and the total number of captures for each individual.

As both white-footed mice and deermice (*Peromyscus maniculatus*) may co-occur at the site, accurate species identification was performed through genetic analysis, requiring collection of a small noninvasive tissue biopsy (5-mm tail clip) that was stored in 95% ethanol at −18°C. Each individual was implanted with a unique passive integrative transponder (PIT) tag (Biomark MiniHPT8; Biomark Inc., Boise, Idaho), inserted under the scruff of the individual's neck prior to release at the site of capture. Tagged individuals were identified during successive captures using a Biomark 601 reader to track individual movement patterns over time. Mass was recorded for each mouse on each successive capture, and all masses for an individual were averaged for analyses. Hind foot length was only measured during 1st capture because the hind feet of white-footed mice have been shown to reach adult form by the 8th or 9th day and adult length within 28 days after birth. Because juveniles typically enter the trappable population 22 days after birth (Millar et al. 1979; Guetzow and Judd 1981), foot size is unlikely to have varied between captures. This justified using foot length as a fixed linear covariate (see below). All animal handling procedures were approved by The University of Tulsa's Animal Care and Use Committee (TU-0041) and conformed to published American Society of Mammalogists guidelines for the use of wild mammals in research (Sikes et al. 2016).

DNA extraction and species identification.—Genomic DNA was extracted from tail biopsies using the Gentra Puregene DNA extraction kit (Qiagen, Germantown, Maryland) and then
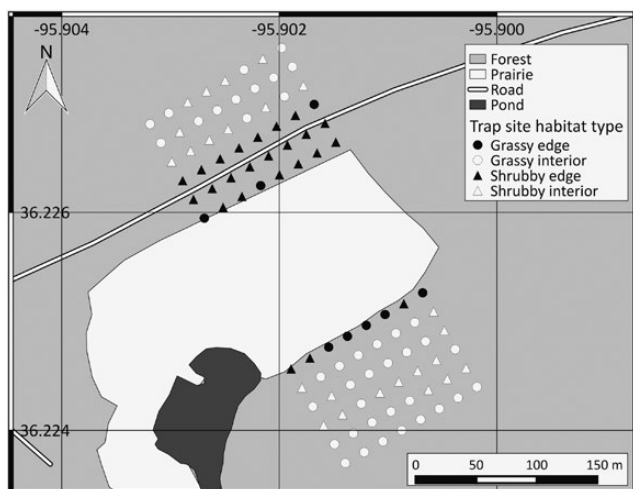
stored at −18°C prior to use. Species identity was confirmed using species-specific mtDNA primers, following Rogic et al. (2013).

Statistical analysis.—Multi-state modeling (Hestbeck et al. 1991; Brownie et al. 1993) using the program MARK (White and Burnham 1999; Cooch and White 2016) was used to estimate daily survival and transition probabilities of white-footed mouse individuals among habitat types. MARK uses encounter histories to compute maximum likelihood estimates of survival, recapture, and transition probabilities. Each model is compared against other models and ranked according to fit using the 2nd-order variant of the Akaike Information Criterion (AIC$_c$—Akaike 1973; Sugiura 1978; Burnham and Anderson 2002). The model with the lowest AIC$_c$ value is considered the best model (Burnham and Anderson 2002). Overdispersion in the data was addressed by calculating a median *c*-hat in MARK ($\hat{c}$ = 1.30) for the fully parameterized (single-state) Cormack–Jolly–Seber model and using that *c*-hat to adjust parameter variances and infer model fit (based on the resulting QAIC$_c$) in subsequent multi-state analyses.

We categorized the forest into the following habitat types that corresponded to multiple states in our analyses: edge versus interior, and grassy versus shrubby. Each forest trapping site could be assigned to 1 of 4 categories (Fig. 1), which represented the state for an individual upon each capture. However, we had to conduct 2 separate multi-state analyses, 1 involving edge versus interior states, and another with grassy versus shrubby states, as the sample size (number of individuals caught) was not sufficient to use all 4 states in a single analysis.

Trapping sites located ≤ 15 m from the edge of the prairie and forest interface and the road and forest interface were assigned to the edge state, whereas trap points located > 15 m from these edges were assigned to the interior state (Fig. 1). We chose 15 m as the cutoff point between edge and interior habitat types because white-footed mouse densities have been shown to change over 15-m intervals (Cummings and Vessey 1994; Wolf and Batzli 2002). Using this method, 33% of the traps were assigned to the edge state and 67% were assigned to the interior state (Fig. 1).

The ground cover of the forest consisted of a patchwork of inland sea oats (*Chasmanthium latifolium*). Trapping sites for which *C. latifolium* made up at least 65% of the surrounding ground cover within 1 m² of the trap were assigned to the grassy habitat state (Fig. 2). All other trapping sites were assigned to the shrubby habitat state. The ground cover of shrubby sites ranged from shrubs to forbs and included areas of relatively bare ground, covered with woody leaf litter (Fig. 2). Plant species diversity measured in the prairie portion of the Oxley Nature Center showed that areas consisting exclusively of grass had species diversity (as measured by the Shannon Index) that was about one-half that of areas with more forbs and invasive shrubs (C. R. Brown, pers. obs.). Using our classification scheme, 50% of the traps were assigned to the grassy state and 50% were assigned to the shrubby state.

We conducted multi-state analyses following Lebreton and Pradel (2002), in which the survival parameter is denoted *S*;

Fig. 2.—Examples of grassy (above) and shrubby (below) forest habitat types.

recapture parameter, *p*; and habitat-transition (or movement) parameter, Ψ. For each parameter, the effect of time was held constant, as captures were not numerous enough to model strict time-dependence or even that based on broader categories such as month only. We allowed parameters to be dependent on sex, habitat type (habitat), average mass (mass), and hind foot length (foot). We first determined the main factors affecting survival and recapture and then modeled factors affecting habitat-transition probability using our best-fitting survival and recapture parameterizations. As in most mark-recapture studies (e.g., Brown et al. 2016), we measured local apparent (relative) survival only, and emigration out of the study area could not be distinguished from mortality. Once the best-fitting transition parameterization was determined, we retried different combinations of factors potentially affecting survival while using our best-fitting recapture and transition parameterizations (see Supplementary Data SD1 and SD2). We generally use the term "movement" in a statistical sense to describe transitions between habitat states (sensu Lebreton and Pradel 2002).

Potential predictors of transition probability that we tested included average mass and hind foot length. These were modeled as continuous linear coefficients in MARK. Although mass could vary across capture occasions, use of an average

value is one way to handle continuously varying covariates that are unknown on the occasions when an individual is present but not captured (Bonner and Schwarz 2006). We also modeled average mass as a quadratic coefficient (mass^2) because studies have shown that individuals toward either extreme of the body-size spectrum may be at a disadvantage, especially in relation to survival (Blanckenhorn 2000; Covas et al. 2002). Interactions among linear covariates (mass * foot) were also modeled. Correlated variables can negatively affect model selection by individually producing similar fits to the data (Freckleton 2011). However, little colinearity between average mass and hind foot length was detected (r^2 = 0.129), so both variables were used as independent predictors (Vergouw et al. 2010). As estimated ages based on characteristics such as pelage color, body size, or reproductive condition are not always reliable (Kunz et al. 1996), age effects were not tested.

RESULTS

A total of 325 captures of white-footed mice was made during 6,697 trap nights from March through December 2015. These consisted of 75 white-footed mouse individuals (49 males, 26 females). Maximum distance moved between trapping sites for 30 males averaged (± *SE*) 52.2 (± 4.7) m, ranging from 19.1 to 103.5 m. For 19 females, maximum distance averaged (± *SE*) 42.7 (± 6.7) m, ranging from 18.5 to 114.2 m. Maximum distance moved was unaffected by sex ($F_{1,43}$ = 0.20, P = 0.20), body mass ($F_{1,43}$ = 0.93, P = 0.34), or foot length ($F_{1,43}$ = 2.57, P = 0.12), varying significantly only with the number of times an individual was captured ($F_{1,43}$ = 26.10, P < 0.0001, analysis of covariance). Maximum distance increased as the total number of captures increased (β ± *SE* = 3.550 ± 0.695).

Survival and recapture.—The best-fitting model for each habitat analysis contained an effect of sex on daily survival probability (Tables 1 and 2). Models that pooled the sexes or separated the habitat types had higher QAIC$_c$ values, making them poorer fits (e.g., models 12, 14, 15, 27, 28, 30 versus models 1, 9, 24; Tables 1 and 2). Models including an effect of individual mass and foot length on survival had lower QAIC$_c$ scores than those that included 1 or none of these covariates (e.g., models 1, 17 versus models 6, 9, 10, 21, 24, 29; Tables 1 and 2). The top models did not include mass squared (e.g., models 4, 18 versus models 1, 17; Tables 1 and 2).

Survival probabilities were estimated from the best-fitting model for each analysis. Females were more likely to survive than males on a day-to-day basis (female S ± *SE* = 0.994 ± 0.002; male S ± *SE* = 0.988 ± 0.003 for both models). Mass had a positive effect on survival (β ± *SE* = 1.023 ± 0.337 for the edge-interior model; β ± *SE* = 1.041 ± 0.336 for the grassy-shrubby model), whereas foot length had a negative effect (β ± *SE* = −0.502 ± 0.243 for the edge-interior model; β ± *SE* = −0.504 ± 0.244 for the grassy-shrubby model; Figs. 3A–D).

For daily recapture probability, the best-fitting model for each analysis contained an effect of sex, habitat type, and mass (Tables 1 and 2). Recapture probability was highest for intermediate-mass mice and lower for mice at either end of the distribution (λ ± *SE* = −0.583 ± 0.244, β ± *SE* = −1.12 ± 0.280 for the edge-interior model; λ ± *SE* = −0.527 ± 0.189, β ± *SE* = −0.972 ± 0.223 for the grassy-shrubby model). Actual recapture probabilities showed that mice in interior and grassy habitats were more likely to be recaptured than mice in the edge and shrubby habitats, and males were more likely to be recaptured than females on a day-to-day basis (p ± *SE* for: female,

Table 1.—Representative multi-state models to assess the effect of sex, edge and interior forest habitat types (habitat), average mass (mass), average mass squared (mass^2), hind foot length (foot), and an average mass and hind foot length interaction (mass * foot) on daily survival (*S*) and habitat-transition (Ψ) probabilities in 75 white-footed mice (*Peromyscus leucopus*) individuals, captured at the Mary K. Oxley Nature Center, Oklahoma, during 2015[a] (*k* = number of estimable parameters; ω = Akaike model weight).

Model #[b]	*S*: sex	*S*: habitat	*S*: mass	*S*: mass^2	*S*: foot	Ψ: sex	Ψ: habitat	Ψ: mass	Ψ: mass^2	Ψ: foot	Ψ: mass * foot	ΔQAIC$_c$	*k*	ω[c]
1	X		X		X	X	X	X		X		0.00	16	0.24
2	X		X		X	X	X	X	X	X		1.08	17	0.14
3	X		X		X	X	X					1.34	14	0.12
4	X		X	X	X	X	X	X		X		2.06	17	0.09
5	X		X			X	X			X		2.20	15	0.08
6	X		X			X	X	X		X		2.58	15	0.07
7	X		X		X		X					4.38	12	0.03
8	X		X		X	X	X	X				7.42	15	0.01
9	X					X	X	X		X		7.82	14	0.00
10	X				X	X	X	X		X		9.79	15	0.00
11	X		X		X	X						10.48	12	0.00
12						X	X	X		X		10.85	14	0.00
13	X		X		X							11.39	11	0.00
14		X				X	X	X		X		95.59	12	0.00
15	X	X				X	X	X		X		96.86	14	0.00
16	X		X		X	X	X	X		X	X	11,620.38	14	0.00

[a]The effect of time was held constant. Covariates included in each model are denoted with an "X".
[b]All models have the following recapture (*p*) covariates: sex, habitat, mass, and mass^2.
[c]ω values do not sum to 1 because only a subset of the models evaluated are shown here.

Table 2.—Representative multi-state models to assess the effect of sex, grassy and shrubby forest habitat types (habitat), average mass (mass), average mass squared (mass²), hind foot length (foot), and an average mass and hind foot length interaction (mass * foot) on daily survival (S) and habitat-transition (Ψ) probabilities in 75 white-footed mice (*Peromyscus leucopus*), captured at the Mary K. Oxley Nature Center, Oklahoma, during 2015[a] (k = number of estimable parameters; ω = Akaike model weight).

Model #[b]	S: sex	S: habitat	S: mass	S: mass²	S: foot	Ψ: sex	Ψ: habitat	Ψ: mass	Ψ: mass²	Ψ: foot	Ψ: mass * foot	ΔQAIC$_c$	k	ω[c]
17	X		X		X	X	X	X		X		0.00	14	0.37
18	X		X	X	X	X	X	X		X		2.07	15	0.13
19	X		X		X	X	X	X	X	X		2.19	15	0.12
20	X		X		X	X	X	X		X	X	2.20	15	0.12
21	X		X			X	X	X		X		2.69	13	0.10
22	X		X		X	X	X					4.55	13	0.04
23	X		X		X	X						6.89	12	0.01
24	X					X	X			X		8.46	12	0.01
25	X		X		X	X				X		8.54	13	0.01
26	X		X		X	X	X					8.61	14	0.00
27						X	X	X		X		9.75	11	0.00
28		X				X	X	X		X		9.91	11	0.00
29	X				X	X	X	X		X		10.45	13	0.00
30	X	X				X	X	X		X		10.64	13	0.00
31	X		X		X							33.73	11	0.00
32	X		X		X	X						39.56	14	0.00

[a]The effect of time was held constant. Covariates included in each model are denoted with an "X".
[b]All models have the following recapture (p) covariates: sex, habitat, mass, and mass².
[c]ω values do not sum to 1 because only a subset of the models evaluated are shown here.
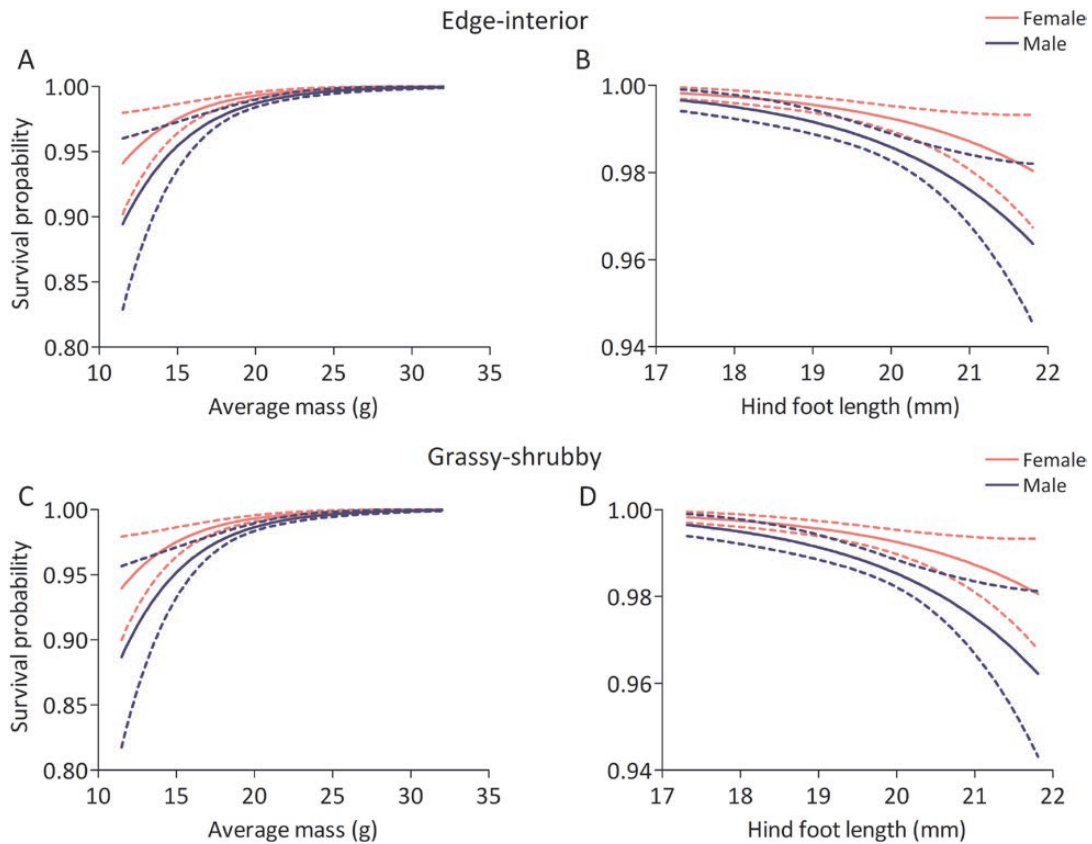

Fig 3.—Effect of average mass (A, C) and hind foot length (B, D) on the probability of daily survival of white-footed mice (*Peromyscus leucopus*) captured at the Mary K. Oxley Nature Center, Oklahoma, during 2015, when comparing edge and interior habitat types (A, B) and grassy and shrubby habitat types (C, D). In A and C, the effect of mass is plotted for the mean value of hind foot length; in B and D, the effect of hind foot length is plotted for the mean value of mass. Solid lines represent the predicted probability of female or male daily survival, and dotted lines represent the 95% *CI*s. A and B are based on model 1 (Table 1), while C and D are based on model 17 (Table 2).

edge = 0.125 ± 0.036; female, interior = 0.261 ± 0.056; male, edge = 0.221 ± 0.031; male, interior = 0.969 ± 0.037; female, grassy = 0.502 ± 0.135; female, shrubby = 0.115 ± 0.025; male, grassy = 0.982 ± 0.025; male, shrubby = 0.311 ± 0.034).

Transitions between forest edge and interior.—The best-fitting edge-interior multi-state models all contained an effect of habitat type and sex on daily habitat-transition probability (Table 1), whereas models that pooled the sexes or the habitat types had higher QAIC$_c$ values, making them poorer fits (e.g., models 7, 11, 13 versus model 3; Table 1). Those including an effect of individual mass and foot length on transition revealed lower QAIC$_c$ scores than models that included 1 or none of these covariates (e.g., model 1 versus models 3, 5, 8; Table 1). Models that included mass squared or an interaction between average mass and hind foot length also were not well supported (e.g., models 2, 16 versus model 1; Table 1).

Habitat-transition probabilities were estimated from the best-fitting edge-interior model (Table 3). The data revealed that transition was sex-biased, and that the probability of transition from the interior to the edge was greater than that from edge to the interior. Females were 11–26× more likely to remain in a habitat type than they were to change habitats. In contrast, males were only 1.5–7× more likely to remain in the same habitat type. Males showed a greater probability of moving from the interior to the edge habitat than from the edge to the interior, even though interior habitat was twice as abundant (Fig. 1). Mass had a negative effect, and foot length a positive effect, on transition probability from edge to interior habitats (β ± *SE* = −0.559 ± 0.274 and 0.434 ± 0.215, respectively; Figs. 4A and 4C).

Transitions between grassy and shrubby habitats.—The better-fitting grassy-shrubby multi-state models all contained an effect of habitat type on daily transition probability but did not contain an effect of sex (Table 2). Models that pooled the habitat types or separated the sexes had higher QAIC$_c$ values (e.g., models 26, 31, 32 versus models 23; Table 2). Those that included an effect of individual mass and foot length on transition often revealed lower QAIC$_c$ scores than those including 1 or none of these covariates (e.g., model 17 versus models 22, 25, 31; Table 2). The top model did not include mass squared or an interaction between average mass and hind foot length (e.g., models 19, 20 versus model 17; Table 2).

Habitat-transition probabilities were estimated from the best-fitting grassy-shrubby model (Table 3). Individuals were 9× more likely to stay within the shrubby habitat type than to move from shrubby to grassy habitats even though the availability of these forest habitat types was equal (Fig. 1). In contrast, individuals were slightly more likely to move from grassy to shrubby habitat than to remain within the grassy habitat type. Mass showed a negative effect on habitat transition (β ± *SE* = −0.828 ± 0.264), whereas foot length showed a positive effect (β ± *SE* = 0.468 ± 0.181; Figs. 4B and 4D).

DISCUSSION

Through multi-state modeling of mark-recapture data collected over a 10-month period, we assessed the influence of habitat type, sex, and body size on the daily survival and habitat-transition probabilities of white-footed mice in a relatively complex forest habitat. Females were more likely to survive than males on a day-to-day basis, while mass had a positive effect and foot length a negative effect on daily survival. Sex and body size affected the daily probability of an animal moving among the forest edge and the interior. Females were more likely to remain within a single habitat type than males, and mass had a negative effect and foot length a positive effect on daily habitat-transition probability. When a habitat transition did occur, it was most likely to be from interior to edge habitat. Body size appeared to affect daily transition probability among grassy and shrubby habitats, with individuals most likely to remain at the shrubby sites and leave the grassy habitat. Mass had a negative effect on daily transition between habitats, whereas foot length had a positive effect.

Habitat effects.—*Peromyscus leucopus* is believed to prefer structurally complex habitat (Myton 1974; Barry and Francq 1980; Kaufman et al. 1983; Barnum et al. 1992); thus, we predicted that mice would be more likely to move to and stay within edge and shrubby habitats than to move to and stay within interior and grassy habitats. The results revealed a pattern of habitat fidelity, with mice generally preferring to remain within a single habitat type; however, when transitions between habitats occurred, they were more likely in the direction of interior to edge and grassy to shrubby. Habitat fidelity can be beneficial, especially during the dispersal stage of an individual's life. Opting to move into or through familiar habitat reduces the costs (e.g., increased predation risk, delayed reproduction) associated with detecting or assessing suitable habitat

Table 3.—Sex-dependent habitat-transition probabilities and standard errors (± *SE*)[a] for 75 white-footed mice (*Peromyscus leucopus*), captured at the Mary K. Oxley Nature Center, Oklahoma, during 2015, dependent upon direction of transition between edge and interior or grassy and shrubby forest habitat types. Movement probabilities were estimated from model 1 (Table 1) and model 17 (Table 2).

From	To interior	To edge	To grassy	To shrubby
Female, edge	0.037 ± 0.023	0.963 ± 0.023		
Female, interior	0.923 ± 0.044	0.077 ± 0.044		
Male, edge	0.112 ± 0.022	0.888 ± 0.022		
Male, interior	0.641 ± 0.064	0.359 ± 0.064		
Both sexes[b], grassy			0.477 ± 0.064	0.523 ± 0.064
Both sexes[b], shrubby			0.098 ± 0.017	0.902 ± 0.017

[a]For all values, the 95% *CI*s did not overlap zero.
[b]There was no significant sex effect on these transitions.
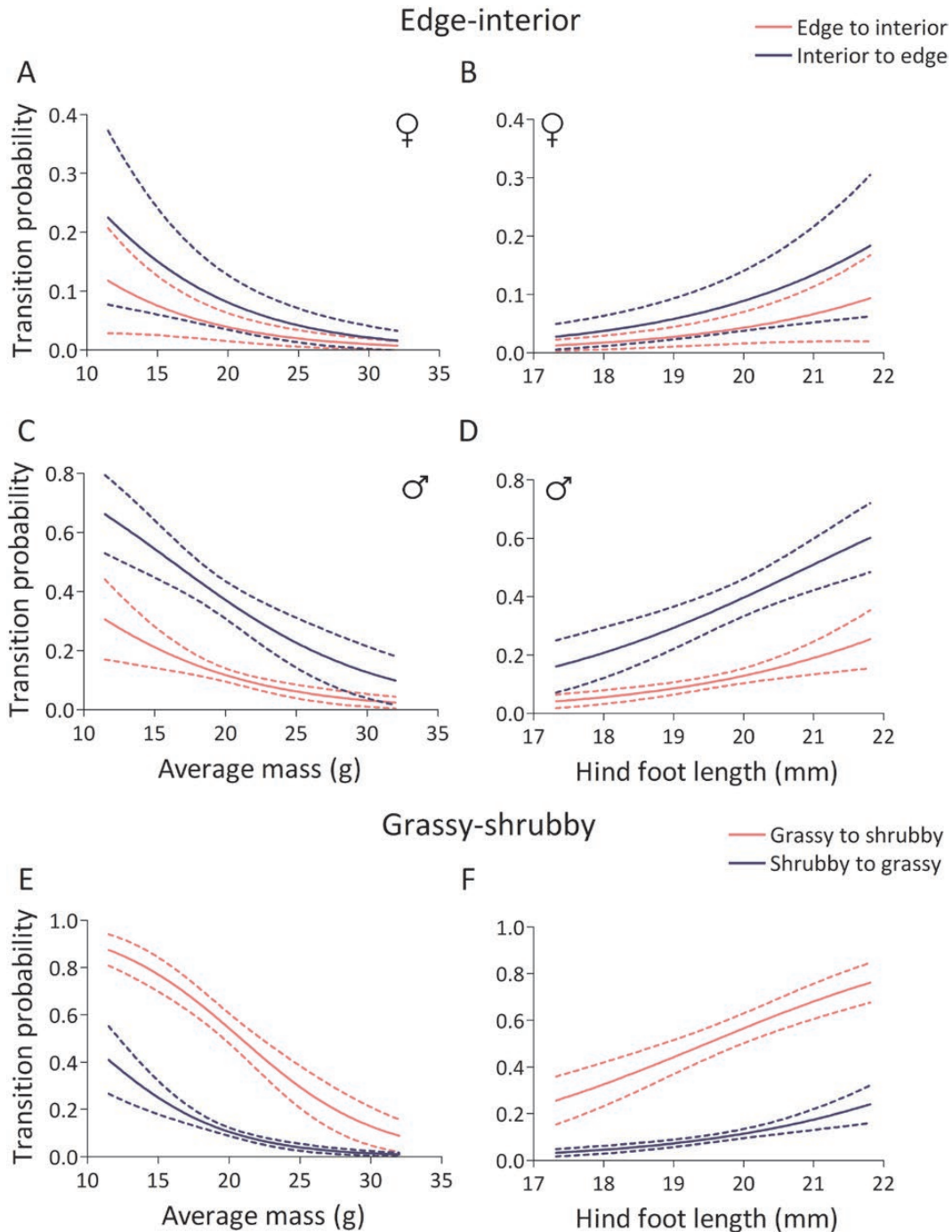
Fig. 4.—Effect of average mass (A, C, E) and hind foot length (B, D, F) on probability of a transition from edge to interior habitat (A–D) and from grassy to shrubby habitat (E, F) in white-footed mice (*Peromyscus leucopus*) captured at the Mary K. Oxley Nature Center, Oklahoma, during 2015. In A, C, and E, the effect of mass is plotted for the mean value of hind foot length; in B, D, and F, the effect of hind foot length is plotted for the mean value of mass. For A–D, solid lines represent the predicted probability of a transition from interior to edge habitat or from edge to interior habitat. For B and D, solid lines represent the predicted probability of moving from shrubby to grassy habitat or from grassy to shrubby habitat. Dotted lines represent the 95% *CI*s. A–D are based on model 1 (Table 1), while E and F are based on model 17 (Table 2). There was no sex effect on transitions among grassy and shrubby habitats (E, F).

(Davis and Stamps 2004; Clobert et al. 2012). Furthermore, individuals can enhance their performance when they rely on habitat-specific foraging experience and predator recognition in familiar habitat (Griffin 2004; Stamps and Swaisgood 2007; Davis 2008).

The finding that white-footed mice lack a strong fidelity to grassy habitat is in line with previous studies of the species (Getz 1961; Kaufman et al. 1983; Barnum et al. 1992; Dooley and Bowers 1996). Mice may avoid grass as a strategy to reduce predation risk (Barnum et al. 1992), or they may simply prefer

shrubby habitat and therefore are more likely to move away from grassy areas. Grassy habitat might offer less food compared to shrubby habitat, which contains more vertical habitat structure and allows for greater species diversity of plants (Wiens 1974; Edwards 1983) and greater availability of fruits, seeds, and insects that are consumed by white-footed mice (M'Closkey and Fieldwick 1975; Wolff et al. 1985; Anderson et al. 2003; Meikle and Wilder 2005).

Our edge-interior movement results are interesting because there has been debate over whether edge habitat is considered higher quality for white-footed mice than interior habitat. Forest edges often contain a greater density of understory vegetation, which white-footed mice have been shown to prefer (Myton 1974; Dueser and Shugart 1978; Kaufman et al. 1983; Drickamer 1990), compared to the interior forest (Cummings and Vessey 1994; Anderson et al. 2003). The edge may also have a higher abundance of food compared to the interior (Wilder and Meikle 2005). Observed differences in reproductive fitness, with edge habitat containing females with more litters, more juveniles per female, and a greater proportion of reproducing females, further support the edge as a higher quality habitat (Dooley and Bowers 1996; Wolf and Batzli 2002; Wilder and Meikle 2005, 2006). In at least one case, however, maternal survival and reproductive success were greatest in the forest interior (Morris 1991, 1996), potentially resulting from increased parasitism, predation, and exposure to more extreme winter temperatures at the edge (Wolf and Batzli 2001, 2004; Wilder et al. 2005).

Sex effects.—Significant sex effects on daily habitat-transition probability were revealed in the edge-interior comparison but not for the grassy-shrubby one. Females showed strong habitat fidelity. The relationship for males was, however, weaker, particularly when comparing the probability of going from interior to edge habitats. Habitat fidelity for females may be a reflection of their home-range size, which tends to be smaller than for males and more dependent on resource needs for reproduction (Hansen and Batzli 1978) or more spatially focused around a nest site. Home-range size of males, in contrast, appears mostly dependent on access to multiple mates and the need to travel to find these mates (Kirkland and Layne 1989). As the area of use decreases, we would expect the likelihood of multiple habitat types within the home range to also decrease. This correlation would be especially so for edge and interior habitat types because their distribution is not as patchy as the grassy and shrubby habitats, which exist as a mosaic throughout the forest.

Furthermore, a female's mean squared distance from the center of its activity increased with distance from the edge, potentially resulting from a reduction in food and nest sites within the interior habitat (Klein and Cameron 2012). This suggests that the edge is of higher quality than the interior, but if so, why did we not see a female preference for the edge? One possibility is that the edge may already be densely populated with females holding small territories, preventing other females from moving into the edge (Anderson et al. 2006). Little information on the typical densities of females in these habitat types

exists to allow comparisons with our present data set (Anderson et al. 2006; Klein and Cameron 2012).

While no difference in male use of habitat along an edge to interior gradient has previously been reported (Klein and Cameron 2012), the higher proportion of reproductive females reported within edge habitat (e.g., Dooley and Bowers 1996; Wolf and Batzli 2002; Wilder and Meikle 2005, 2006) suggests that movement of males into edge habitats, as we found, may be reproductively advantageous.

Body-size effects.—Smaller-bodied individuals are often juveniles or behaviorally subordinate animals (Dewsbury 1979). Both categories are considered most likely to disperse or move when compared to adults and dominant individuals (Gaines and McClenaghan 1980; Van Horne 1982). Our findings support an increased likelihood of smaller-bodied individuals (i.e., those of lower body mass) moving between habitats. Likely drivers are density-dependent processes, where at high population densities dominant (higher-mass) individuals occupy the highest quality habitat and force subordinate individuals into habitat of lower quality (Fretwell 1972). Multiple studies have suggested that aggressive adult white-footed mouse force dispersal by juveniles and subordinate animals and discourage their immigration (Metzgar 1971; Hansen and Batzli 1978; Van Horne 1982; Halama and Dueser 1994).

We found that mice with larger feet, independent of body mass, were more likely to make a habitat transition. This might reflect larger-footed animals having increased running efficiency associated with longer hind limbs, allowing for increased stride length with reduced energetic costs of cycling the limbs (Myers and Steudel 1985; Steudel 1990; Carrano 1999; Kelly et al. 2006). More efficient locomotion efficiency could then lead to the larger-footed animals simply being more active in general, and thus for this reason might be more likely to be caught in a different habitat. However, we found little evidence that foot length (or mass or sex) affected the maximum distance that individual white-footed mice moved between traps. This would suggest that mice that changed habitats were not in fact inherently more likely to be active (e.g., by virtue of greater locomotion efficiency), and thus they were probably responding to other cues in moving to a different habitat. Why larger-footed individuals would be more likely to move from grassy to shrubby habitats, and from forest interior to edge, is unclear at present.

Fitness consequences.—Dispersal is considered a risky strategy (Clobert et al. 2012) that negatively affects survival (e.g., Metzgar 1967; Ambrose 1972; Yoder et al. 2004; Brown et al. 2008; Forrester et al. 2015), with the risk often attributed to reduced foraging efficiency or decreased ability to detect or avoid predators in unfamiliar areas. Our findings reveal a pattern where females, heavier individuals, and individuals with shorter feet have a higher probability of daily survival than males, lighter individuals, and individuals with longer feet, respectively. Interestingly, the phenotypic categories least likely to survive were also the categories with the highest probability of transitioning between habitat types, suggesting that movement to a different habitat is indeed risky for white-footed

mice. The survival costs associated with switching among habitat types could be one reason why individuals of this species seem to prefer particular habitats (Kaufman et al. 1983; Barnum et al. 1992).

Although our sample size did not allow us to consider an effect of date, such effects probably exist. Given the annual population cycle of white-footed mice in which population density peaks in the fall or winter and levels out in the spring (Adler and Tamarin 1984), daily survival is probably reduced in the winter and spring and increases in the summer and fall. White-footed mice are known to nest communally in the winter and establish individual home ranges in the spring with the onset of the breeding season (Nicholson 1941). Such seasonal shifts in home range could be reflected in habitat-transition probabilities, if, for example, the home range during the breeding season encompasses greater habitat patchiness than a home range during the nonbreeding season (or vice versa). We encourage future studies to consider the spatial autocorrelation of trap-habitat designations in order to separate transitions related to spatial context and those related to actual behavioral decisions of the individual.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—List of all multi-state models used to assess the effect of sex, edge and interior forest habitat types (habitat), average mass (mass), average mass squared (mass^2), hind foot length (foot), and an average mass and hind foot length interaction (mass * foot) on daily survival (*S*), recapture (*p*), and habitat-transition (Ψ) probabilities in 75 white-footed mice (*Peromyscus leucopu*s) captured at the Mary K. Oxley Nature Center, Oklahoma, during 2015. The effect of time was held constant. Covariates included in each model are denoted with an "X".

Supplementary Data SD2.—List of all multi-state models used to assess the effect of sex, grassy and shrubby forest habitat types (habitat), average mass (mass), average mass squared (mass^2), hind foot length (foot), and an average mass and hind foot length interaction (mass * foot) on daily survival (*S*), recapture (*p*), and habitat-transition (Ψ) probabilities in 75 white-footed mice (*Peromyscus leucopus*) captured at the Mary K. Oxley Nature Center, Oklahoma, during 2015. The effect of time was held constant. Covariates included in each model are denoted with an "X".

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