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Habitat selection of a large carnivore, the red wolf, in a human-altered landscape

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ABSTRACT

Large carnivores, with their expansive home range and resource requirements, are a good model for understanding how animal populations alter habitat selection and use as human densities and development increase. We examined the habitat selection of red wolves (*Canis rufus*) in North Carolina, USA, where the population of red wolves resides in a mosaic of naturally occurring and human-associated land cover. We used locations from 20 GPS-collared red wolves, monitored over 3 years, to develop resource selection functions at the landscape level. Red wolves selected for human-associated land-cover over other land-cover types. Red wolves also selected areas near secondary roads. However, red wolves avoided areas with high human density, and avoidance of natural land-cover types decreased as human density increased; this interaction was strong enough that red wolves selected for natural land-cover types over human-associated land-cover types at relatively high human density. Similarly, avoidance of natural land-cover types decreased when they were near secondary roads. These results suggest that red wolves will use human-associated landscapes, but modify their habitat selection patterns with increased human presence. Such findings suggest that large carnivores such as the red wolf may not strictly require habitats devoid of humans. In a world with rapid human-alteration of habitat, understanding how increasing human density and development impact habitat selection is vital to managing for population persistence of large carnivores and maintaining top-down ecological processes.

1. Introduction

As human populations and development increase, animal populations must either be confined to diminishing areas of natural habitat or adapt and persist in a mosaic of human-altered and naturally occurring habitats. Large carnivores are highly susceptible to human-associated change in habitat due to their expansive home ranges and longer generation times (Mladenoff et al., 1997). Thus, some populations of large carnivores will need to persist in a mosaic of human-altered and naturally occurring habitats. Species unable to survive in human-altered habitats are likely to require constant management including intensive monitoring of individuals, population trends, and biological seasons. Thus, an understanding of how large carnivores select habitats in a mosaic of human-altered and naturally occurring land cover is critical to the appropriate allocation of resources for conservation and management of such populations. Furthermore, such information may be useful for identifying areas with high potential for species persistence.

Red wolves (*Canis rufus*) once ranged across eastern North America from Florida to southern Canada and central Texas to the Atlantic Ocean (Phillips et al., 2003). Currently, most of the historic range of red wolves contains high human densities and vast expanses of human-altered habitat. Only a single reintroduced population of <150 red wolves designated as nonessential experimental by the US Fish and Wildlife Service currently exists in the wild in a habitat mosaic consisting of naturally occurring and human-associated land cover (Phillips et al., 2003). Basic ecological research on habitat selection by red wolves in the wild prior to reintroduction was limited due to small population size and difficulties in differentiating the few remaining red wolves from hybrids and coyotes *Canis latrans* (Phillips et al., 2003). Previous researchers suggested that red wolves historically occupied moist, densely vegetated habitats, including virgin pine and lowland hardwood forests, coastal prairies, and marshes (Phillips et al., 2003). However, these studies of red wolf habitat selection were conducted on small, remnant populations persisting in limited naturally occurring environments. More recent studies have attempted to understand habitat selection of red wolves in their more current, human-dominated habitat (Chadwick et al., 2010; Hinton and Chamberlain, 2010). However, no study has examined how habitat selection by red wolves is influenced by natural and anthropogenic landscape attributes. A better understanding of

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how red wolves select resources in a mosaic of human-altered and naturally occurring habitat is critical to management of the current population and to future reintroductions of red wolves.

A great deal of research has examined habitat use by gray wolves *Canis lupus* and the potential for expansion of reintroduced and fragmented populations to adjacent areas (Corsi et al., 1999; Harrison and Chapin, 1998; Mladenoff et al., 1995, 1997, 1999; Wydeven et al., 2001). The major consensus among these studies is that large social carnivores like wolves are unable to persist in areas of high human and road densities (Mech, 2006; Mladenoff et al., 1995, 1999; Oakleaf et al., 2006; Wydeven et al., 2001), putatively due to high wolf mortalities in such areas (Corsi et al., 1999). Studies in Europe suggested that such variables mask a prevailing negative human attitude towards wolves. Instead increasing human and road densities themselves do not prohibit colonization and persistence of wolves (Corsi et al., 1999), but rather it is the ill intentions of humans that limit wolves in such areas (Wydeven et al., 2001; Murray et al., 2010; Rutledge et al., 2010). Indeed, wolves may select human-altered as readily as naturally occurring land-cover (Treves et al., 2004; Mech, 2006) if the selection process is unimpeded by such things as negative human actions against wolves (Mladenoff et al., 1997). Several studies have suggested that wolves are highly capable of persisting in human-altered landscapes and possibly even perceiving increased mortality risk associated with human density and development and adjusting habitat use accordingly (Bateman and Fleming, 2012; Lesmerises et al., 2012; Llaneza et al., 2012). Since being reintroduced in 1987, red wolves have selected among various human-altered and naturally occurring land-cover types, with population levels increasing for the first decade and here lately having stabilized due to the population likely having reached the carrying capacity of the recovery area (Phillips et al., 2003). Preliminary evidence suggests that red wolves, if unimpeded by human actions, will readily select human-altered land-cover (Chadwick et al., 2010); such evidence agrees with selection patterns of gray wolves (Mech, 2006).

We examined 2nd order habitat selection (Johnson, 1980) of red wolves in the sole remaining wild population, with the intent of understanding how red wolves select and use habitats associated with humans. Specifically, we studied habitat selection by red wolves over several seasons, determined how habitat selection varied with human density and development, and examined how these environmental factors influence habitat selection by red wolves at the landscape level. We predicted that red wolves would select agricultural fields over other land-cover types due to concentration of white-tailed deer (*Odocoileus virginianus*), the primary prey of red wolves (Dellinger et al., 2011), in agricultural fields as a consequence of a nearly year round growing season. We also predicted that red wolves would avoid areas of increasing human density but likely select areas near secondary roads (e.g., dirt and gravel roads), which coincides with recent findings (Lesmerises et al., 2012; Llaneza et al., 2012), potentially due to ease of travel and increased visibility for hunting.

2. Study area

This study occurred within the Red Wolf Recovery Experimental Population Area (RWREPA) on the Albemarle Peninsula in northeastern North Carolina (Fig. 1). The RWREPA is currently home to the only wild population of red wolves in the world. The study area consisted of >4900 km^2 of federal, state, and private lands in five counties (Hyde, Tyrrell, and parts of Dare, Washington, and Beaufort). Federal lands within the study area included Alligator River National Wildlife Refuge, Pocosin Lakes National Wildlife Refuge, Swan Quarter National Wildlife Refuge, Mattamuskeet National Wildlife Refuge, and a bombing range shared by the United States

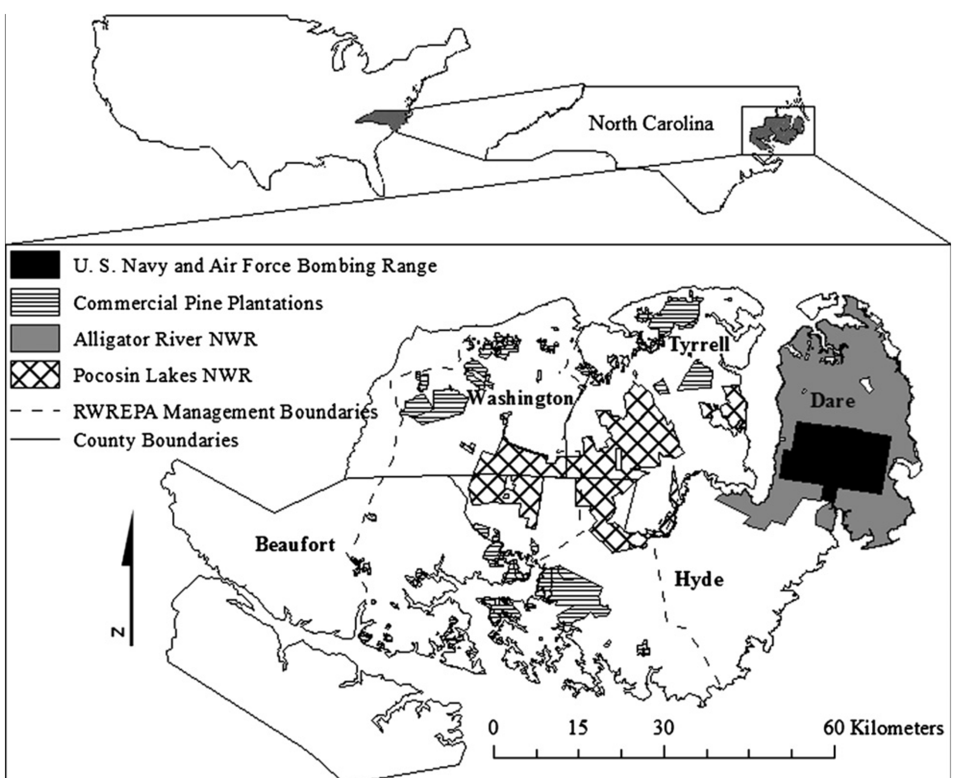

Fig. 1. Map of RWREPA in northeastern North Carolina with county boundaries, RWREPA management boundaries, and location of federal, commercial, and private lands (white areas), 2007–2011.

Navy and Air Force. State lands included numerous game management properties, while private lands were primarily timber plantations and agricultural fields.

Land cover in the study area included several human-associated types: agricultural fields (30%); early successional fields (20%); and commerical pine plantations (15%); as well as a few naturally occuring types: pocosin *Pinus serotina* and *Persea palustris* (15%); lowland forests *Nyssa* spp., *Liquidambar styraciflua*, *Acer rubrum*, and *Chamaecyparis thyoides* (10%); and wetlands (10%). Climate was characterized by four full seasons of nearly equal length with annual precipitation averaging 127 cm. Temperatures averaged 5 °C in winter and 27 °C in summer. Elevation ranged from sea level to 50 m (Hinton and Chamberlain, 2010). Human density averaged 5.75 people/km^2 and ranged from 0 to 795 people/km^2 (US Census Bureau).

3. Materials and methods

3.1. Capturing and radio-collaring of animals

During July 2007 to March 2010, United States Fish and Wildlife Service (USFWS) biologists used padded, number 3, foot-hold traps to capture adult and juvenile red wolves. USFWS biologists fitted red wolves with mortality-sensitive, Lotek GPS 4400S radio-collars (Lotek Wireless, Inc., Newmarket, Ontario, Canada). Red wolves >2 years old were classified as adults, between 9 months and 2 years old as juveniles, and <9 months old as pups. Radio collars were not fitted on pups because pups were too small to safely wear the collars. Following deployment, radio-collars recorded locations every 5 h. Every collar emitted a VHF beacon each day during 0900–1200 h, which allowed animals to be located every 4–8 weeks for remote retrieval of data.

3.2. Home range analyses

We used adaptive nearest neighbor convex hull methods (α-NNCH; Getz et al., 2007) to construct 95% home ranges for each radio-collared animal. We developed rarefaction curves of estimated home range size for each animal to determine if radio-collars had been deployed long enough for estimated home range size to stabilize. Specifically, rarefaction curves were developed such that home range size was calculated for the first week the collar was deployed, the first two weeks, and so on, until all the data for that animal had been included. The home range estimate was deemed to have stabilized if home range size increased <5% with each additional week for at least 12 weeks to at least ensure a seasonal stabilization in home range size.

Because individual wolves within a pack likely exhibit habitat selection patterns that are not independent from each other we only calculated selection coefficients for one individual in each pack. If packs contained multiple radio-collared animals, and one was an alpha animal, then locations from the alpha were used to assess habitat selection. If estimated home range size of the alpha did not stabilize, or an alpha animal was not radio-collared, then locations from the animal monitored for the longest period of time were used to assess habitat selection, conditioned on a stabilized estimate of home range size for that individual. Two packs had no individuals for which cumulative weekly home range size stabilized, likely due to brief monitoring periods, and thus were excluded from analyses of habitat selection. GPS locations from radio-collared individuals not belonging to a pack were included in analyses of habitat selection if individuals were monitored for a sufficient period of time to generate stability in their movements and home range size.

3.3. Habitat selection analyses

We analyzed habitat use at the home range level using a use versus availability approach to determine which habitats had a higher likelihood of being selected by red wolves. Specifically we examined 2nd order habitat selection (Johnson, 1980) by red wolves using resource selection functions (RSFs) which assume that habitat selection patterns are revealed by comparing known (GPS points) to random available locations taken from across the landscape (Manly et al., 2002). We considered used habitats to be all GPS locations from each radio-collared animal that occurred within its respective 95% home range isopleth (McLoughlin et al., 2004). We considered the entire RWREPA as available habitat from which random locations could be taken. Red wolves were well distributed throughout the RWREPA, justifying use of the entire area as available habitat. The number of randomly selected available locations equaled the number of used locations (Klar et al., 2008). Distance to road and water, human density (US Census Bureau, 2010), and land cover type were determined for all locations using GIS. We did not differentiate between primary paved and secondary unpaved roads due to the low density of primary roads (0.12 km/km^2) in the RWREPA. Such a low density of primary roads was thought to have little potential as a meaningful variable for landscape level habitat selection analyses. Land cover types included agricultural fields, wetlands, pine plantations, lowland forests, early successional fields, and pocosin (upland areas covered with evergreen vegetation and inundated with water; McKerrow et al., 2006). Agricultural fields, pine plantations, and early successional fields were human-altered habitats while lowland forests, wetlands, and pocosin were naturally occurring habitats. Our global RSF for habitat selection contained each of the land-cover-type, distance to roads and water, and human density variables, measured at the landscape level, as well as all biologically meaningful interactions (land-cover type by distance to roads, land-cover type by human density, and distance to roads by human density). We designated agricultural fields as the reference land-cover type in the global RSF. Note that no collinearity was found amongst any combination of any of the variables above.

All used or available locations were combined across individuals for analysis. Because we monitored animals for varying lengths of time, and therefore had different numbers of locations, each animal potentially could have influenced the RSFs more or less than other animals (Manly et al., 2002; Klar et al., 2008)). Thus to make sure that no animal biased the global RSFs, we developed preliminary RSFs and used a sampling with replacement method in which each animal was excluded once from calculation of a RSF while all other animals were included. We then compared signs of coefficient estimates of preliminary RSFs to signs of coefficient estimates of the global RSFs. If the signs were the same between coefficient estimates of preliminary and global RSFs, and coefficient estimates of preliminary RSFs were contained within the 95% confidence intervals of the global RSF, then the animal excluded from the preliminary RSF was not deemed to bias the global RSF relative to other animals with respect to the given variable (Gillingham and Parker, 2008).

Akaike's information criterion corrected for small sample sizes (AICc) was used to choose the best RSF from the global model and all possible subsets (Burnham and Anderson, 2002). We excluded 25% of used and random locations from being used in developing the global RSFs and all possible subsets. We used excluded locations to perform a cross-validation and evaluate fit of the best RSFs, as determined by AICc (Johnson et al., 2006). This cross-validation method, shown to be the most appropriate for use-availability RSF models (Johnson et al., 2006), involved first projecting the best-fit RSFs constructed with 75% of the data in a GIS. Next we reclassified RSF values, which ranged from 0 to 1, into 10 equally sized ordinal classes (e.g., 0.0–0.1, 0.1–0.2, etc.) and determined utilization values, based on the mean value and area, for each ordinal class (Johnson et al., 2006). Then we counted the number of used locations in the withheld data that fell in each class and estimated the expected the number of used locations for each class by overlaying the withheld data onto the projected RSF. Finally we performed linear regression and χ^2-square tests to compare expected to observed number of used locations in each class (Johnson et al., 2006). We considered that there was strong agreement between observed versus expected number of used locations, indicating the RSF model was proportional to probability of selection, if the observed versus expected linear regression had a slope significantly different from 0 (i.e., use was not equal to availability) but not significantly different from 1 and the y-intercept was not significantly different from 0 (i.e., the modeled RSF was directly proportional to probability of use). Finally, we considered that a good RSF model would have a high R^2, derived from the linear regression of proportion of observed versus expected number of used locations, and a high Spearman rank correlation coefficient (Johnson et al., 2006).

All statistical analyses were conducted in R 2.11.1 (R Development Core Team, 2010), while spatial analyses were conducted in ArcGIS 10 (Redlands, CA, Copyright 1999–2010 ESRI) and Geospatial Modelling Environment 0.5.3 (Beyer, H.L., Copyright 2001–2010 Spatial Ecology).

4. Results

During July 2007 to March 2010, 17 adult (12 males, 6 females) and 17 juvenile (9 males, 7 females) red wolves were fitted with GPS collars and monitored for between 2 and 30 months, with an average monitoring period of 13 months. The radio-collared animals represented 13 packs and 9 lone individuals that still showed site fidelity as evidenced by stabilized cumulative weekly home ranges.

Rarefaction curves of 95% home range isopleths (Getz et al., 2007) stabilized for all but two animals, data from these 2 animals was not included in RSF calculations. Thus, habitat selection was done based on GPS locations from 20 animals. Signs of all coefficient estimates of all preliminary 2nd order RSFs were no different from signs of coefficient estimates of the global 2nd order RSF. Furthermore, all coefficient estimates of preliminary RSFs were contained within the 95% confidence intervals of the coefficient estimates of the global RSF, indicating no one animal unduly biased the global RSF (Gillingham and Parker, 2008).

We used 32,802 red wolf locations, and an equal number of randomly selected available locations, to construct the RSFs. The best RSF among those considered, as determined by AICc, contained variables for all individual land-cover types, distance to roads and water, human density, an interaction between distance to road and land-cover type (lowland forests, pocosin, and wetlands), and an interaction between human density and land-cover type (pine plantations, lowland forests, and wetlands; Table 1). The AICc weight of the best RSF was 0.28. The three next best RSFs had delta AICc values of <2, suggesting that any of our top four RSFs could potentially be the best RSF (Table 1). Given the similarity and the small delta AICc values of the top four RSFs (Table 1) we averaged the coefficient estimates of the top four RSFs (Table 2; Burnham and Anderson, 2002). Furthermore, given the treatment of each of these RSFs as potentially the best, it is also reasonable to combine AICc weights of these four RSFs which is 0.88, demonstrating a strong ability to predict red wolf habitat use in the RWREPA. Agricultural fields (the reference land-cover type in the model) were selected over all other land-cover types at low human density and in areas close to roads. Odds of habitat being used by red wolves decreased as human density increased, distance to roads increased, and distance to water decreased (Table 2). As distance to roads increased, avoidance of lowland forest, pocosin, and wetland land-cover types by red wolves, relative to other land-cover types, further increased (Table 2). Similarly, as human density increased, avoidance of pine plantations, lowland forests, and wetlands by red wolves, relative to other land-cover type types, decreased (Table 2). However, the interaction between lowland forests and human density only occurs in two of the top four RSFs (Table 1), suggesting that this variable is important but only moderately so relative to the other variables. Coefficient estimates suggest that at 11.1, 27.7, and 10.4 people per km^2, selection for agricultural fields over pine plantations, lowland forests, and wetlands, respectively, switched such that red wolves selected for pine plantations, lowland forests, and wetlands over agricultural fields. The best RSF predicts a patchy distribution of red wolves across the RWREPA (Fig. 2).

We used 10,934 red wolf locations, and an equal number of randomly selected available locations to cross validate our model averaged RSF coefficient estimates (Table 2). For the model averaged RSF, the slope of the linear regression of proportion of observed versus expected locations in each ordinal class was significantly different from 0 (coef. est. = 1.14, SE = 0.18, t_{16} = 6.4, p < 0.01), but not significantly different from 1 (t_{16} = 0.79, p = 0.44). This demonstrates that the model averaged coefficient estimates were proportional to the probability of habitat selection by red wolves and that red wolves do not use habitat in proportion to availability but rather demonstrate habitat selection. Also the Y-intercept of the linear regression was not significantly different

Table 1
Comparison of AICc, ΔAICc, AICc weights, and number of parameters of top 2nd order RSF models.

Model	AICc	ΔAICc	Weights	Parameters
1[a] – 2[b] – 3[c] – 4[d] – 5[e] – 6[f] + 7[g] – 8[h] – (2 × 6) – (3 × 6) – (4 × 6) + (3 × 8) + (4 × 8) + (5 × 8)	21422.93	0.00	0.28	14
1 – 2 – 3 – 4 – 5 – 6 – 7 – 8 – (2 × 6) – (3 × 6) – (4 × 6) + (3 × 8) + (5 × 8)	21423.14	0.21	0.25	13
1 – 2 – 3 – 4 – 5 – 6 – 7 – 8 – (2 × 6) – (3 × 6) – (4 × 6) + (3 × 8) + (4 × 8) + (5 × 8) + (6 × 8)	21424.06	1.13	0.16	15
1 – 2 – 3 – 4 – 5 – 6 – 7 – 8 – (2 × 6) – (3 × 6) – (4 × 6) + (3 × 8) + (5 × 8) + (6 × 8)	21424.69	1.76	0.12	14
1 – 2 – 3 – 4 – 5 – 6 – 7 – 8 – (2 × 6) – (3 × 6) – (4 × 6) – (2 × 8) + (3 × 8) + (4 × 8) + (5 × 8)	21425.93	3.00	0.06	15
1 – 2 – 3 – 4 – 5 – 6 – 7 – 8 – (2 × 6) – (3 × 6) – (4 × 6) – (2 × 8) + (3 × 8) + (5 × 8)	21426.14	3.21	0.06	14

[a] Successional fields.
[b] Pocosin.
[c] Wetlands.
[d] Lowland forests.
[e] Pine plantations.
[f] Distance to roads.
[g] Distance to water.
[h] Human density.

Table 2
2nd Order RSF model averaged coefficient estimates for top four RSFs according to AICc, for habitat use of red wolves in the RWREPA from 2007 to 2011.

2nd Order RSFs		
Coefficient	Estimate	SE
Intercept	0.62	0.04
SF[a]	−0.21	0.09
PC[b]	−0.67	0.09
WL[c]	−0.81	0.08
LF[d]	−0.82	0.11
PP[e]	−0.95	0.08
D2R[f]	-1.29×10^{-03}	1.10×10^{-04}
D2W[g]	2.85×10^{-03}	0.04
HD[h]	−0.08	5.00×10^{-03}
D2R × LF	-2.70×10^{-03}	3.40×10^{-04}
D2R × PC	-2.79×10^{-03}	2.16×10^{-04}
D2R × WL	-2.48×10^{-03}	2.08×10^{-04}
HD × D2R	4.146×10^{-07}	1.87×10^{-04}
HD × PP	0.09	0.01
HD × LF	0.03	0.01
HD × WL	0.08	0.01
HD × PC	-6.29×10^{-03}	0.02

[a] Successional fields.
[b] Pocosin.
[c] Wetlands.
[d] Lowland forests.
[e] Pine plantations.
[f] Distance to roads.
[g] Distance to water.
[h] Human density.

from 0 (coef. est. = −0.01, SE = 0.02, $t_{16} = -0.55$, $p = 0.59$), again indicating that the model averaged RSF was proportional to the probability of habitat selection by red wolves. Agreement between proportion of observed and expected locations within each ordinal class was high with a $R^2 = 0.84$ and $r_s = 0.98$ ($p < 0.01$) demonstrating that the model averaged RSF was able to predict habitat selection by red wolves other than those used to build the RSFs (Johnson et al., 2006).

5. Discussion

The ecology and spatial requirements of many large carnivores, like the red wolf, suggest that recovery and persistence of viable populations, if possible, will likely occur not in small patches of protected habitat, but in a mosaic of protected, managed, and largely human-altered habitats. Simply avoiding human-associated land-cover types may not be possible for such species, as available naturally occurring land-cover types are limited, and often in decline. Thus, large carnivores may be forced to utilize human-associated land-cover types while avoiding negative interactions with humans.

As we predicted, our best RSFs indicated that at the 2nd order level of habitat selection red wolves did avoid areas with high human density. Several studies report avoidance of areas of increasing human densities by gray wolves (Corsi et al., 1999; Oakleaf et al., 2006). Moreover, at low human densities, red wolves selected agricultural fields and cut-over regenerating forests over all other, naturally occurring land-cover types (Table 2). This result is as we predicted but still interesting in itself given that agricultural fields represent human-altered habitat. Selection of human-altered habitats over natural habitats by red wolves could be due to agricultural and early successional fields providing higher food resources to prey species such as white-tailed deer relative to other habitat types, thus helping to concentrate prey species important to red wolves (Dellinger et al., 2011). Recent research in Minnesota and Wisconsin, USA, report gray wolves denning in the middle of hay fields and other areas associated with human activity (Mech, 2006). Red wolves have also been reported denning in agricultural fields near areas of high human activity (Hinton and Chamberlain, 2010).

Similarly, our 2nd order best RSFs also indicated that red wolves prefer areas close to roads (Table 2). This supports our original predictions and recent research (Lesmerises et al., 2012; Llaneza et al., 2012). Most roads in the RWREPA are secondary gravel or dirt roads used for agricultural purposes. Red wolves likely select these secondary roads for hunting due to the greater visibility and mobility

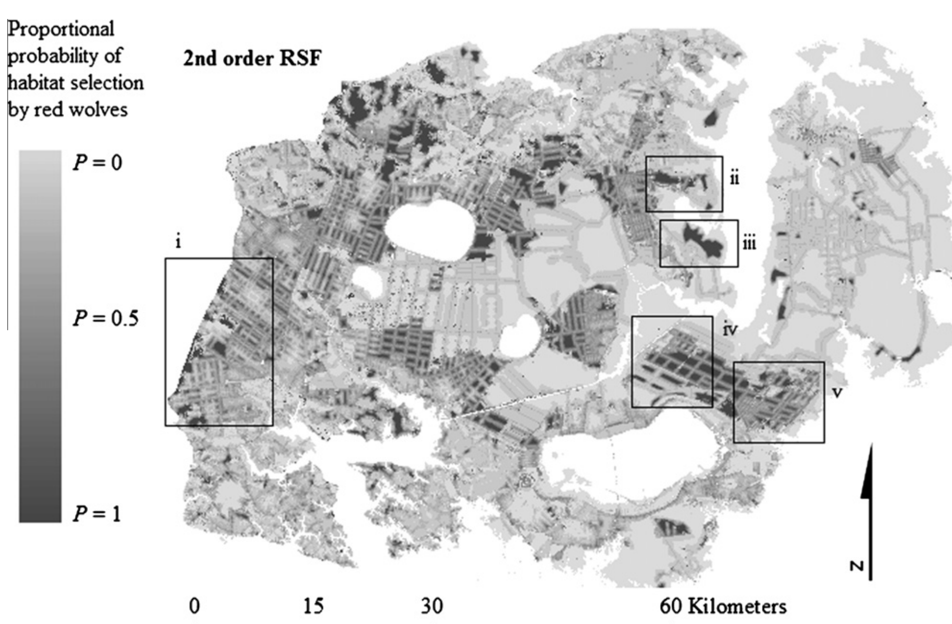

Fig. 2. Proportional probability of habitat selection by red wolves (*Canis rufus*) across the RWREPA in northeastern North Carolina with respect to 2nd order habitat selection, 2007–2011. Map represents our 2nd order RSF model averaged coefficient estimates for top four RSFs according to AICc. (i) Relative location of packs no longer in existence but identified as habitat with high relative probability of occurrence of red wolves; (ii–v) relative location of packs not represented in our dataset but in existence at the time of this study, indicating our top 2nd order RSF can predict potential location of packs not regularly monitored or places where dispersing animals might establish home ranges.

such roads provide a cursorial predator like red wolves. Our third and fourth best RSF included a positive interaction between human density and distance to road (Table 1), suggesting that as human density increased red wolves selected areas further away from roads. It is likely that increasing human density is positively correlated with primary paved roads. These results imply that red wolves can differentiate between high and low traffic roads. But a lack of differentiation between primary and secondary roads in our analyses makes such an interaction difficult to interpret. Gray wolves in Alaska were found to avoid high traffic roads while selecting areas close to secondary roads, presumably for ease of travel and low human use of secondary roads (Thurber et al., 1994).

However, our study revealed that habitat selection by red wolves is influenced by changes in human density and development (i.e., presence of secondary roads). According to our best RSF, as human density increased, strength of avoidance of pine plantations, lowland forests, and wetlands decreased, relative to other land-cover types, including human-associated land cover (Table 2). Thus given this interaction between human density and land-cover type, it is possible that red wolves exhibit some tolerance towards increasing human densities and this trait, if selected for, may permit red wolves to persist within a mosaic of human-altered and naturally occurring habitat. It is possible that this decreased avoidance of normally avoided habitats and, at relatively high human densities, eventual selection of these habitat types over agricultural and early successional fields (Table 2) may indicate a reaction to an increase in potential human-red wolf conflict. Agricultural fields and early successional fields are very open habitats with high visibility. Pine plantations, lowland forests, and wetlands are more heavily vegetated with lower visibility. Red wolves, like other carnivores, may prefer such habitats in relatively higher human density areas where human-red wolf conflicts are possibly more likely (Conde et al., 2010; Lesmerises et al., 2012). Similarly, as distance to roads decreased, avoidance of lowland forests, pocosin, and wetlands decreased relative to other land-cover types (Table 2). Much of the RWREPA is subject to periodic rise in water levels due to proximity to the Atlantic Ocean, resulting in many areas being inundated frequently. Such areas, when inundated, are difficult for red wolves to move through and are also likely avoided by primary prey like white-tailed deer. The above interaction is likely an interaction between distance to roads and surrounding water levels in a given area. Thus, habitats often inundated with water are selected primarily when bisected by roads (Table 2). Where roads are present, these habitats could serve as travel corridors and allow for red wolves to persist in areas where low and high quality habitats are highly interspersed and large parcels of high quality habitats are few. For large carnivores in general, sub-optimal habitats might serve as important routes of dispersal for young adults or travel corridors within an animal's home range, linking habitats necessary for survival and reproduction (Corsi et al., 1999; Harrison and Chapin, 1998; Mech, 2006). Furthermore, large areas of intact high quality habitat may not be as necessary for conservation of some species of large carnivores, if such areas are adequately connected (Harrison and Chapin, 1998; Mech, 2006; Mladenoff et al., 1997).

Research on whether selection of particular land-cover types by large carnivores is affected by human density or roads has been limited. Several previous studies have shown that habitat selection by gray wolves is influenced by human and road densities (Cayuela, 2004; Corsi et al., 1999; Lesmerises et al., 2012; Llaneza et al., 2012; Mladenoff et al., 1999; Oakleaf et al., 2006; Thurber et al., 1994). However, these studies only went as far as to demonstrate that wolves were at higher risks of mortality in areas of high human density and development and actively avoided these areas. We do not suggest negative human attitudes and actions as the sole reason for the limited recovery and conservation of large carnivores. However, we do suggest that large carnivores may select human-altered land-cover types if unimpeded, thus increasing likelihood of recovery in areas in close proximity with humans. Understanding how habitat selection by wolves is affected by changes in human density and overall development could help identify areas of potential human-wolf conflict or direct management for fostering recolonization of large carnivores such as wolves; if public perception allows for such management. Research on gray wolves in the Great Lakes area of the USA revealed that changes in human and road density, and transition from natural to human-altered land-cover types were good predictors of depredation of livestock by gray wolves (Treves et al., 2004). Such an understanding could be used to adjust livestock husbandry practices to reduce human-wolf conflict in such areas.

6. Conclusion

Given that a large percentage of the historic range of the red wolf, and the naturally occurring land-cover therein, has been altered by human activities, future reintroductions and persistence of red wolves will likely require populations to persist in areas dominated by human presence and development. Our results indicate that red wolves will use human-associated land cover types. Red wolves were also shown to shift habitat use as human density and development increased, suggesting they can adjust to changes in these variables. These results also provide support for the idea that other large carnivores can persist in parts of their historic range where a habitat mosaic of human-altered and natural land-cover types now exists. Such results, inherently applicable to the management and conservation of other pack forming large carnivores, can also be applied to solitary large carnivores if one considers that red wolf packs have the same drives and needs as solitary large carnivores: to obtain food, reproduce and raise young, and establish a home range; implying that social and solitary large carnivores can be viewed similarly as units, making our results applicable to all types of large carnivores for conservation and management. Though in the case of large carnivores, including the red wolf, serious conservation efforts are needed to assist the species in recolonizing such areas. These conservation efforts would not only need to assist the given species by way of reintroductions but also serve as mediators; interacting with the local peoples in an attempt to reduce negative social perceptions that are generally associated with such efforts (Oakleaf et al., 2006). We cannot be certain that all large carnivores are capable of persisting in such circumstances. However, our study demonstrates that one large carnivore, the red wolf, is adaptable enough to at least respond to human-related changes in its environment. Managers and conservationists working with large carnivores elsewhere could benefit from understanding how changes in human density and development impact habitat use. The next step is to understand, for species such as the red wolf, the implications of shifts in habitat use in response to changes in human density and development on survival and reproduction.

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