

Density-dependent habitat selection varies between male and female African elephants

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Highlights

- Fine-grain habitat selection of elephants varies with density and between sexes.
- Males and females differ in density-dependent responses to human infrastructures.
- Habitat selection makes males more likely involved in human-wildlife conflicts.
- Sex- and density-dependent selection can give critical info to orient conservation.

Abstract

Habitat selection models are the basis of an increasing number of conservation and management programs. Decision-makers rely on accurate models to assess animal distribution over space and time, and to recommend suitable actions that can alleviate human-wildlife conflicts. Despite a rapidly growing number of field studies on habitat selection, there remains a paucity of empirical evidence that selection is a density-dependent process that can impact males and females differently. Based on 11 years of monitoring, we demonstrate that the response of African elephants (*Loxodonta africana*) to land-cover types varied with population size, and that density-dependent adjustments differed between sexes. Specifically, our longitudinal follow-up of GPS-collared elephants revealed that elephants

gradually decrease their selection for open woodlands and forests, as the population increased and the availability of palatable browse species decreased. Both sexes – though males more strongly – increased their travel rate together with their relative probability of selection of roads for travel. Also, elephants displayed a density-dependent increase in their selection of infrastructures, a response that was stronger for males than females. The risk of human-elephant conflicts thus increased with population size, with males being particularly prone to be involved in such conflicts. Overall, we provide rare empirical evidence that density-dependence in fine-grain habitat selection can differ between sexes. This information can be critical to accurately forecast potential human-wildlife conflicts, and for taking targeted and effective conservation and management actions.

Keywords: Elephant; density-dependent habitat selection; human-wildlife conflict; game reserve; sex-related habitat selection

1. Introduction

Habitat selection studies play a central role in wildlife conservation and management. Animal distribution results from individuals attempting to maximize fitness through the selective use of habitat resources (McLoughlin et al. 2006). On this basis, habitat selection studies have been used to define, albeit with certain caveats, habitat quality and identify critical resources for wildlife populations (Arditi and Dacorogna 1988; Morris 2003; Johnson 2007). Habitat selection is recognized as a complex process, involving behavioral responses to a broad range of habitat features that can vary between sexes and with population size (Shannon et al. 2006; Herfindal et al. 2009; Merkle et al. 2015). The effectiveness of management and conservation actions at reducing human-wildlife conflicts thus may depend on whether or not such elements of complexity have been considered in management planning. For example, because male Asian elephants (*Elephas maximus*) are more likely to raid crops than females (Sukumar and Gadgil 1988), management actions focusing on males (e.g., culling) should be more effective. By contrast, human-bison conflicts involving the Sturgeon River bison (*Bison bison*) are mostly caused by female-dominated groups, and become particularly concerning when the population exceeds social carrying capacity (sensu Cherry et al. 2019). Accordingly,

proposed management actions focus on the movement paths of adult females leading to conflict areas, as well as on altering the availability of selected resources (Simon and Fortin 2019).

Differences in habitat selection between males and females have been underscored for multiple large herbivores, including moose *Alces alces* (Bjorneraas et al. 2012), elk *Cervus elaphus* (Paton et al. 2017), and Mediterranean mouflon *Ovis gmelini musimon* × *Ovis* sp. (Marchand et al. 2015). For example, rams of the Mediterranean mouflon select areas rich in high-quality forage, whereas females with young selected areas with dense protective cover (Marchand et al. 2015). Male moose display stronger avoidance of roads than females (Laurian et al. 2012), because humans are less likely to be encountered far from roads and males experience higher hunting pressure (Paton et al. 2017). As for other large herbivores (McLaren and Green 1985; Fortin and Andruskiw 2003; Cameron et al. 2005), female African elephants (*Loxodonta africana*) are more sensitive than males to the presence of humans (McComb et al. 2014), and, accordingly, males appear more likely to approach and spend time near human infrastructure (Cook et al. 2015; Orrick 2018). Sex-specific habitat selection can thus create differences in the impact of males and females on ecosystems, a situation that provides opportunities to fine-tune management actions. Nonetheless, habitat selection studies commonly focus on individuals of a single sex (e.g., Boyce et al. 2003; Gagné et al. 2016; Simon et al. 2019) or integrate observations from males and females without discrimination (e.g., Chetkiewicz and Boyce 2009; Matawa et al. 2012).

An additional level of complexity comes from density-dependent changes in animal-habitat relationships. Theory of density-dependent habitat selection stipulates that animals should increasingly use habitats of relatively poor quality or adopt opportunist tactics, rather than selective ones, as conspecific density increases (Rosenzweig 1981; Morris 2003). This theoretical principle has received empirical support (Rozen-Rechels et al. 2015; McLoughlin et al. 2016). For example, elk and moose select food-rich, mixed-wood forests at low conspecific density, but as density increases, they start selecting lower quality habitat, such as agricultural fields for elk and built-up areas for moose (Matthiopoulos et al. 2015).

Density dependence remains largely overlooked in multi-variable habitat selection studies, in part because those studies are often conducted over too short periods of time to observe important fluctuations in population density (McLoughlin et al. 2010). A number of

studies have evaluated density-dependent habitat selection, but did not assess potential variations in habitat selection between males and females following an increase in conspecific densities (e.g., Fortin et al. 2008; Rozen-Rechels et al. 2015). The few studies that did assess such variations found significant differences in density-dependent selection between sexes, such as in red deer, *Cervus elaphus* (Clutton-Brock et al. 1987) and white-tailed deer, *Odocoileus virginianus* (Kie and Bowyer 1999). Overlooking density-dependent effects should result in an incomplete understanding of how human activities shape animal distribution.

The reintroduction of African elephant in Ithala Game Reserve (IGR), a 297 km² reserve in South Africa, exemplifies the challenges inherent to the reintroduction of wildlife in enclosed areas. From 1990 to 1993, 50 elephants were reintroduced in IGR. The population had increased to 56 by 2000 (Wiseman et al. 2004), before reaching *ca.* 190 individuals in 2018, a number that largely exceeded the estimated carrying capacity of 120 elephants. Following this increase, palatable woody vegetation has decreased while unpalatable species increased (Wiseman et al. 2004; Gordijn et al. 2012). This situation illustrates well the challenge of maintaining megaherbivores within fenced areas without compromising the conservation of other wildlife species. Detailed knowledge of habitat selection dynamics can help meet this challenge.

We used 11 years of monitoring of radio-collared African elephants in the IGR to develop sex- and density-dependent models of habitat selection. While accounting for multiple natural-cover types, the models assessed density-dependent differences in the reaction of male and female elephants to land cover types rich in woody vegetation (i.e., open woodlands and forests) and to human-related landscape features (i.e., roads and infrastructure such as staff houses). We derived a set of predictions from foraging and habitat selection theory, and from the ecology of fear. Foragers can benefit from reducing their use of a given habitat type when the food it offers decreases in quantity or quality (Stephens and Krebs 1986; Fortin et al. 2015). Accordingly, we predict that P₁) the selection of open woodlands and forests will decrease with the increase of elephant density because of the concurrent decline in palatable woody vegetation across the IGR (Wiseman et al. 2004; Gordijn et al. 2012). Basic habitat selection theory predicts that, as population increases, competition for food resources should increase and foragers should become

more opportunistic by expanding into more marginal habitats (e.g., ideal free distribution or ideal despotic distribution: Fretwell and Lucas 1969; Morris 1994; Becker et al. 2021). This expansion and the faster depletion of resource patches due to higher competitor density should lead to more frequent inter-patch movements, and hence to higher travel rates (marginal value theorem: Charnov 1976; Laguë et al. 2012). Accordingly, we predict that P₂) elephants will increase their travel as the population grew, which P₃) will result in higher probability of selection of roads for travel efficiency, especially by males because of their lower fear of humans. Indeed, consumers commonly further adjust their foraging decisions and distribution dynamics to their landscape of fear (e.g., Kotler et al. 2004; Bleicher 2017; Simon et al. 2019). With population growth, individuals may increase their use of relatively risky habitats not only because of increased competition (hence lower encounter rate with suitable food items, Fortin et al. 2015), but also because safety in numbers or habituation to humans may decrease their fear (Dehn 1990; Krause and Ruxton 2002; Hebblewhite et al. 2005). Given the resources available near human infrastructures in IGR, we predict that P₄) the selection of infrastructures will increase with elephant density, and that the increase will be steeper for males because they are less fearful of humans than females.

2. Methods

2.1. Study area

Our study took place in IGR, a protected area of 29 653 ha in KwaZulu-Natal, South Africa (27° 45'S 31° 37'E). The reserve has a network of roads used for game drives, but some roads are restricted to 4×4 vehicles. Although there is only one main tourist facility, other human infrastructure, including staff houses, workshops, and offices, are dispersed throughout IGR (Appendix A, Fig. A.1).

Mean annual rainfall is ca. 790 mm and mean annual temperature is 18.5°C. The wet season (November to February, which was extended from October to March for the analysis) is hot with January mean daily minimum and maximum temperatures of 14.9°C and 26.7°C, respectively. Mean monthly rainfall during this period are usually > 100 mm. The dry season (May to August extended from April to September) is cool and dry, with July mean daily minimum and maximum temperatures of 4.0°C and 20.4°C, respectively, and < 20 mm of

rain per month. The transition periods (March-April and September-October) are characterized by intermediate temperatures and precipitation. Vegetation in IGR is dominated by bushveld (i.e., well-grassed plains dotted by dense stands of trees and shrubs) with thorny species (cover *ca.* 50%), grasslands (> 30%), riparian vegetation (8%), and forests (< 3%; a more complete description is provided in van Rooyen and van Rooyen 2008). Water is accessible year-round, as many springs, rivers, and streams flow through the reserve.

2.2. *Elephant locations*

A total of 16 GPS-collared elephants were tracked between August 2005 and January 2017. Collars were installed on seven males and nine females (each from different breeding herds), each one followed for a mean of *ca.* 3 years. GPS-collared elephants spent *ca.* 4% of their time within 100 m of other collared elephants. Given this low percentage, subsequent analyses considered as statistically independent the data collected from different elephants/herds.

2.3. *Habitat variables*

We defined eight land-cover types from a detailed vegetation map of the protected area (van Rooyen and van Rooyen 2008): bushveld, open woodlands, grasslands, old grasslands, riparian areas, forests, cliffs, and infrastructure (Appendix A, Fig. A.1). Spatial information on the road and river networks, and on the fence surrounding IGR were also available. Slope was derived from a 20-m Digital Elevation Model, using the function `terrain` of the R package `raster` (Hijmans and van Etten 2012).

2.4. *Statistical analysis*

We developed typical resource-selection functions (RSF, McLoughlin et al. 2010) by contrasting the observed GPS locations ($n = 58\,188$) of collared elephants with an equal number of locations randomly drawn within the reserve. Observed locations were scored 1 and random locations 0. Each location was characterized by its land cover type, its slope, and its distance to the nearest river, nearest road and nearest fence. Land-cover types were categorical variables, with bushveld being considered the reference category. The analysis also considered the sex (M) of the collared individuals, and population density (N) during the year in which a given location was taken. Because the number of elephants in the reserve

was not estimated each year, we interpolated the missing data based on the regression between the number of elephants and time since their introduction (Fig. 1). All continuous covariables were standardized (i.e., mean = 0, SD = 1) to facilitate the comparison of their relative probability of selection (*sensu* Lele et al. 2013).

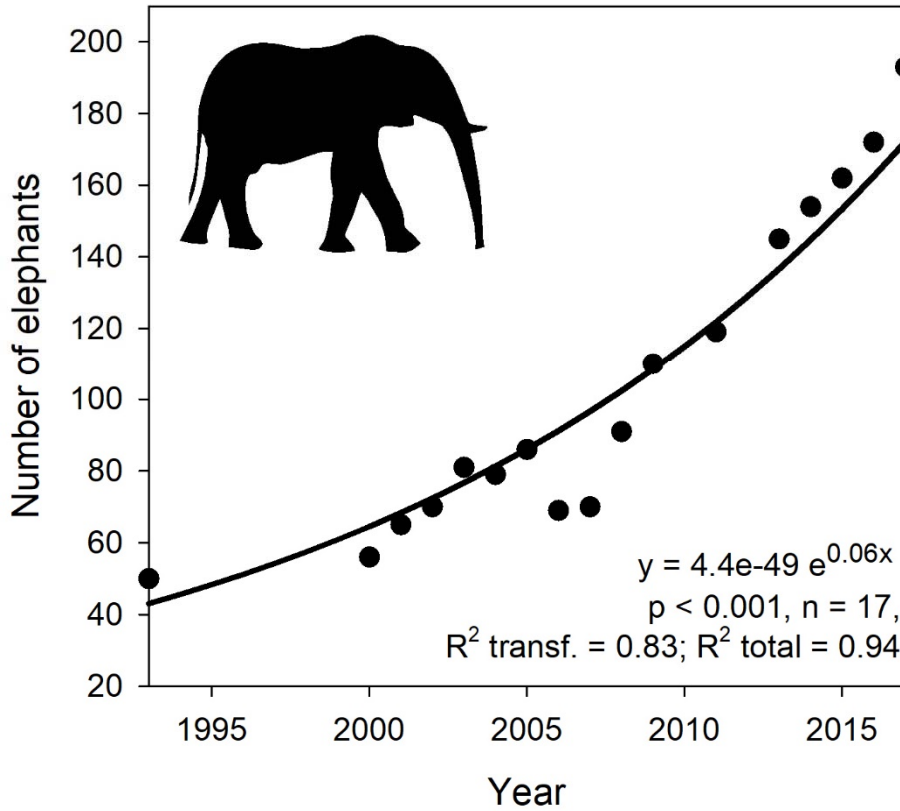


Figure 1. First-order autoregressive model (AR1) relating the number of elephants to time in Ithala Game Reserve, South Africa. R^2 transf. is the R^2 statistic for the regression of transformed variables adjusted for the estimated autocorrelation, whereas R^2 total is the model R^2 .

Following McLoughlin et al. (2010), we used interaction terms to assess whether selection of human-related variables (i.e., distance to road, distance to fence and infrastructures) varied with elephant density and between sexes. RSFs took the form:

$$w(\mathbf{x}) = \exp(\beta_0 + \beta'_{1-7}\mathbf{x}_{1-7} + \beta_{MM} + \beta_{NN} + \beta'_{8-11}\mathbf{H}_{1-4} + \beta'_{12-15}\mathbf{H}_{1-4}M + \beta'_{16-19}\mathbf{H}_{1-4}N + \beta_{MNMN} + \beta'_{20-23}\mathbf{H}_{1-4}MN), \quad \text{Eq. 1}$$

where β_{1-7} are regression coefficients for covariates \mathbf{x}_{1-7} (grassland, old grassland, cliff, riparian, slope, distance to the nearest river, distance to the nearest fence), β_{8-11} are individual coefficients for \mathbf{H}_{1-4} : open woodland, forest, infrastructure, distance to the nearest road. Double ($\beta_{12-15}\mathbf{H}_{1-4}\mathbf{M}$; $\beta_{16-19}\mathbf{H}_{1-4}\mathbf{N}$; β_{MNMN}) and triple interaction terms ($\beta_{20-23}\mathbf{H}_{1-4}\mathbf{MN}$) are required to test whether the response to habitat features \mathbf{H}_{1-4} differs between sexes and with elephant density. For example, $\beta_{12-15}\mathbf{H}_{1-4}\mathbf{M}$ test if males (i.e., $\mathbf{M} = 1$ in Eq. 1) select individual features of \mathbf{H}_{1-4} differently than females under average population size, i.e., $\mathbf{N} = 0$ is the average because, as the other continuous variables, \mathbf{N} was standardized. Accordingly, if $\mathbf{N} = 0$ then $\beta_{16-19}\mathbf{H}_{1-4}\mathbf{N} = \beta_{\text{MNMN}} = \beta_{20-23}\mathbf{H}_{1-4}\mathbf{MN} = 0$. By contrast, the triple interactions (β_{20-23}) assess if males and females selected individual habitat features \mathbf{H}_{1-4} differently and if this difference further changes with conspecific density. To simplify in interpretation of the RSFs, we provide a figure displaying changes in RSF scores, $\exp(w[\mathbf{x}])$, as a function of the different human-related habitat features. RSF scores are proportional to the relative probability of selection (Lele et al. 2013).

We compared environmental variables between observed and random locations using generalized estimating equations (GEEs), which provide standard errors adjusted for serial autocorrelation in the observations of each animal (Koper and Manseau 2009). RSFs were estimated separately for the dry (April to September) and wet (October to March) seasons. Following an inspection of the residuals for non-linear trends, we assessed whether log transformation or squared-root transformation of distance to nearest river, distance to nearest road, or population size could improve model adjustment by contrasting the quasi information criterion (QIC, Pan 2001) of competing models. Table 1 only reported the two best RSFs (one for each season), which had the lowest QIC by least 6.6. No multicollinearity problems were detected in any RSF, with variance inflation factor never exceeding 3.96 (Belsley et al. 1980) for any covariate or interaction term. We evaluated if both models were robust to 5-fold cross validation (Boyce et al. 2002), with robust models yielding high average \bar{r}_s ($n = 100$).

Finally, we evaluated the relationship between the distance moved during the 4-hour relocation interval (in m / h) using a mixed-effects model with individual as random effect. The seasonal models including the independent variables $\ln(\mathbf{N})$, Sex (\mathbf{M} : dichotomous variable, female being the reference category), and their interaction.

Table 1. Parameter estimates (β) with robust confidence intervals (CI) of resource selection functions of elephants in wet and dry seasons, in Ithala Game Reserve, KwaZulu-Natal, South Africa. Averaged ($n = 100$) Spearman rank correlation coefficient (\bar{r}_s) from 5-fold cross-validation and their standard deviations (SD) are also presented.

Covariable	Wet season β (95% CI)	Dry season β (95% CI)
β_0 : Intercept	0.17 (0.09:0.25)	0.05 (-0.004:0.10) ^Φ
β_1 : Grassland	-1.04 (-1.28:-0.80)	-0.36 (-0.51:-0.20)
β_2 : Old grassland	-0.89 (-1.12:-0.66)	-0.79 (-0.89:-0.69)
β_3 : Cliff	-0.29 (-0.71:0.12) ^{NS}	-0.91 (-1.51:-0.31)
β_4 : Riparian	0.32 (0.22:0.42)	0.22 (0.04:0.41)
β_5 : Slope	-0.30 (-0.37:-0.24)	-0.18 (-0.24:-0.13)
β_6 : Distance (in m) to river	-0.27 (-0.36:-0.18)	-0.41 (-0.49:-0.33)
β_7 : Distance (in m) to fence	0.10 (-0.02:0.23) ^{NS}	-0.11 (-0.20:-0.02)
<i>Assesment of density-dependent and sex-related habitat selection</i>		
β_N : ln(Elephant number, N)	0.02 (0.01:0.04)	0.009 (-0.004:0.02) ^{NS}
β_M : Male (M)	-0.04 (-0.11:0.02) ^{NS}	-0.10 (-0.16:-0.03)
β_{MN} : M \times ln(N)	-0.05 (-0.09:-0.02)	-0.05 (-0.10:-0.01)
β_8 : Open woodland	-0.22 (-0.38:-0.06)	0.22 (0.03:0.40)
β_9 : Forest	0.38 (0.22:0.54)	1.01 (0.88:1.13)
β_{10} : Infrastructure	-1.34 (-1.83:-0.85)	-0.85 (-1.08:-0.61)
β_{11} : Distance (in m) to road	0.01 (-0.03:0.05) ^{NS}	-0.21 (-0.28:-0.14)
β_{12} : Open woodland \times M	-0.64 (-1.06:-0.22)	-0.36 (-0.57:-0.15)
β_{13} : Forest \times M	0.17 (-0.23:0.58) ^{NS}	-0.35 (-0.66:-0.04)
β_{14} : Infrastructure \times M	2.23 (1.58:2.88)	2.31 (1.90:2.71)
β_{15} : Distance to road \times M	-0.25 (-0.43:-0.08)	-0.27 (-0.37:-0.18)
β_{16} : Open woodland \times ln(N)	-0.16 (-0.25:-0.06)	-0.01 (-0.11:0.13) ^{NS}
β_{17} : Forest \times ln(N)	-0.26 (-0.41:-0.11)	-0.13 (-0.29:0.02) ^Φ
β_{18} : Infrastructure \times ln(N)	0.31 (-0.04 :0.65) ^Φ	0.28 (0.06 :0.55)
β_{19} : Distance to road \times ln(N)	-0.07 (-0.11:-0.04)	-0.05 (-0.12:0.01) ^Φ
β_{20} : Open woodland \times M \times ln(N)	-0.21 (-0.41:-0.01)	-0.35 (-0.49:-0.20)
β_{21} : Forest \times M \times ln(N)	0.41 (0.14:0.67)	-0.12 (-0.59:0.33) ^{NS}
β_{22} : Infrastructure \times M \times ln(N)	0.54 (-0.005:1.08) ^Φ	0.75 (0.36:1.14)
β_{23} : Distance to road \times M \times ln(N)	-0.07 (-0.16:0.01) ^Φ	-0.10 (-0.19:0.002) ^Φ
<i>Validation \bar{r}_s (SD)</i>	0.99 (0.01)	0.99 (0.02)

Notes: Distance to road was log-transformed for the wet season. All continuous variables have been standardized (mean = 0, SD = 1). The reference categories are bushveld for land-cover types, and females for sexes.

^{NS}Indicates that 95% and 90% confidence intervals both include 0.

^ΦIndicates that 95% confidence intervals include 0, but that 90% confidence intervals exclude 0.

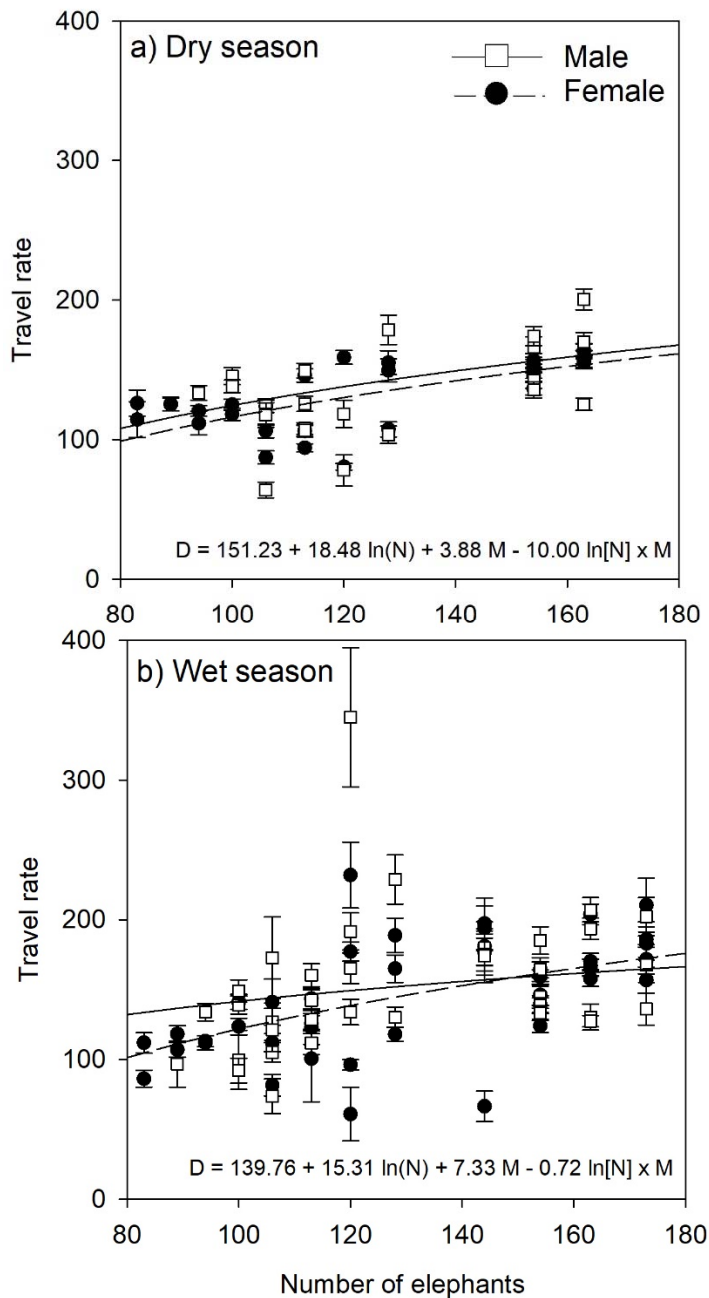


Figure 2. Mixed-effects model relating the distance that elephants moved during a 4-h relocation interval (D , in m/h) to conspecific density (log-transformed N) and sex ($M = 1$ for male and 0 for female) in a) dry and b) wet seasons, in Ithala Game Reserve, KwaZulu-Natal, South Africa. All terms had $P < 0.001$, with the exception of $\ln(N) \times M$ ($P = 0.68$) in dry season, and M ($P = 0.08$) in wet season. Average (\pm standard error) are displayed for each radio-collared individual and each population size.

3. Results

In both seasons, male and female elephants increased their movement rate as the population grew (Fig. 2). During the dry season, the density-dependent increase was similar between sexes (i.e., β of $\ln(N) \times M$ not significantly different from 0, Fig. 2a), but males maintained a higher travel rate (i.e., β of $M > 0$). During the wet season, males traveled at a higher rate than female at low density but the rate became similar at high density (Fig. 2b); females thus increased their speed more steeply as conspecific density increased (i.e., β for $\ln(N) \times M < 0$).

RSFs revealed that elephants selected areas near rivers and avoided steep slopes in both seasons (Table 1). Relative to bushveld (the reference category), elephants also avoided grasslands of any type throughout the year, while they selected riparian areas. In both seasons (though marginally in the dry season), male and female elephants decreased their relative probability of selection of open woodlands as the population grew (β_{16} and $\beta_{17} < 0$, Table 1; Fig. 3), a relationship that remained stronger for males throughout the year ($\beta_{20} < 0$). Males and females also displayed this density-dependent response towards forests in the dry season (Fig. 3a), but not in the wet season (Fig. 3b). Instead, males increase their relative probability of selection of forests as the number of elephants increased ($\beta_{21} > 0$, Table 1). The analysis further indicates that the relative probability of selection of infrastructure increased with elephant density in the dry season ($\beta_{18} > 0$, Table 1, Fig. 3a), a density-dependent response that was stronger for males than females ($\beta_{22} > 0$, Table 1). The same density dependent trends (given the 90% CI) were observed during the wet season.

In the dry season, individuals had a higher relative probability of selection of areas closer to roads when the population was of average size (i.e., when standardized $\ln[N] = 0$, which was ~ 135 elephants). This latter result can be inferred because setting $\ln[N] = 0$ removes all density dependent parameters, and because β_{11} and $\beta_{15} < 0$ (Table 1). During the dry season, little response to roads was observed at low elephant densities (Fig. 2). At high elephant densities, however, both sexes tended to have a higher probability of occurrence near than far from roads. This difference was especially strong in the wet season given that, in the dry season, $\beta_{19} < 0$ only under 90% confidence intervals (Table 1). Overall, the density-dependent response was marginally stronger for males than females ($\beta_{23} < 0$ under 90% confidence intervals, Table 1; Fig. 3).

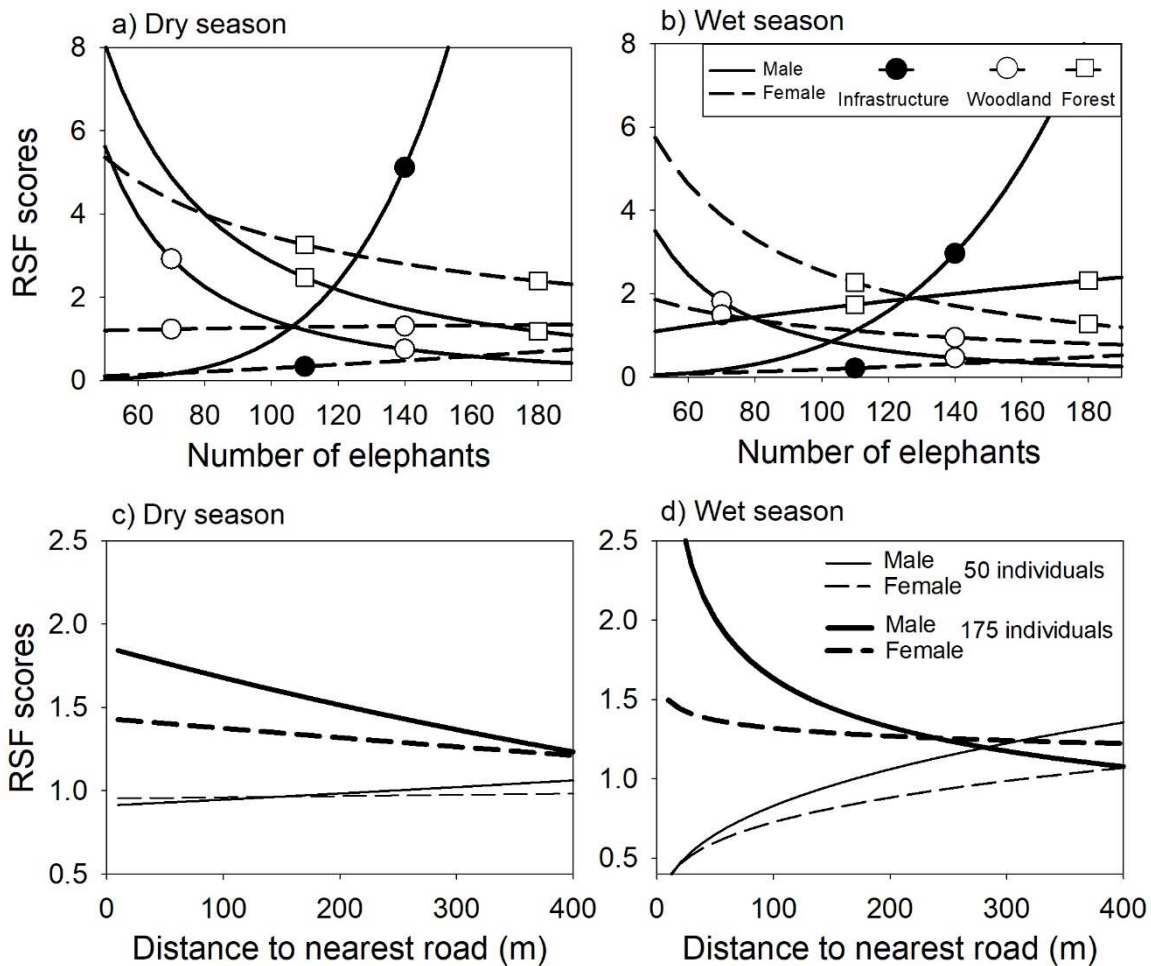


Figure 3. Effect of sex and elephant density on the response of elephants to habitat features in dry and wet seasons in Ithala Game Reserve, South Africa. RSF scores ($\exp[\text{coefficient}]$) are proportional to the relative probability of selection, and they were calculated from the models presented in Table 1. Female selection is represented by a dashed line whereas male selection is represented by a solid line. Relative probability of selection of open woodlands, forests and infrastructures in a) dry season and b) in wet season; c) Relative probability of selection with respect to roads in dry season and d) wet season for males and females with 50 and 175 conspecifics.

4. Discussion

Our study provides empirical evidence that density-dependent habitat selection can differ between sexes. While such assessment remains relatively rare, especially in studies of fine-grain habitat selection (van Beest et al. 2014), it can provide valuable insights to anticipate and then develop guidelines notably to resolve potential conflicts between wildlife and humans. For example, we found that males had a higher probability of selecting human-related habitat features compared to females, and that they also show a stronger density-

dependent response to these features. Their reaction to human-related features makes males particularly prone to human-elephant conflicts, especially under high conspecific density.

4.1. Density-dependent and sex-related habitat selection

Our conclusions on density-dependent and sex-related habitat selection by elephants are based on multivariable habitat selection models that accounted for basic responses to IGR vegetation mosaic. For example, elephants avoided grasslands, which can explain the relatively low proportion of grasses in their diet in IGR (Wiseman et al. 2004), something that contrasts with observations made in other reserves (Codron et al. 2006; O'Connor and Page 2014). Elephants also made selective use of riparian areas during the wet season, which are characterized by a relatively dense canopy that can offer high-quality forage and shade, two elements sought out by elephants (Holdo 2003; Ntumi et al. 2005; Kinahan et al. 2007). Thus, seasonal shifts in diet choice may help explain fundamental differences in habitat selection (Gordijn et al. 2012; Shrader et al. 2012; Ward et al. 2017). Density-dependent and sex-related habitat selection of elephants were largely consistent with expectations from foraging and habitat selection theory (e.g., Fortin et al. 2015; Becker et al. 2021), and from the ecology for fear (e.g., Kotler et al. 2004; Bleicher 2017). As we predicted, we observed a density-dependent decrease in the selection of elephants for open woodlands (P_1) and forests (P_2). Since their reintroduction into the reserve, the elephant population has increased as did other populations of browsers (Wiseman et al. 2004). The overall increase in competitors has reduced the availability of palatable woody species (Wiseman et al. 2004; Gordijn et al. 2012), which led us to predict a density-dependent decrease in the relative probability of selection of open woodlands and forests (P_1). This prediction held for both males and females in the dry season and for females in the wet season. Males, however, did not follow this pattern in the wet season, which could reflect the fact that they tend to be solitary or move in small groups (Skinner and Chimimba 2005). Thus, low levels of food availability should not affect them as much as the larger breeding herds. Moreover, the larger body size of males would allow them to obtain adequate nutritional gains from lower quality food (i.e., Jarman-Bell Principle, see Jarman 1974). The general decrease in browse availability across the reserve was also expected to trigger an increase in movements (P_2). Accordingly, we observed both male and female elephants increasing their travels as the population grew. This increase came with a density-dependent augmentation in the relative

probability of selection of roads (consistently with P₃). In addition to making travel easier, elephants may be attracted to roads because of the vegetation growing along their sides.

When resource depletion triggers a decrease in the use of a given habitat type (open woodland and forest in our case), foragers should gain by broadening their habitat selection (Fryxell and Lundberg 1997; Fortin et al. 2015). Accordingly, food depletion in floodplain has stimulated the expansion of waterbuck (*Kobus ellipsiprymnus*) into savanna (Becker et al. 2021). Here we show that, as predicted (P₄), elephants expanded their habitat selection by gradually increasing the selection of human infrastructures as the population grew. The increase was steeper for males than females, which may reflect differences in trade-offs between food and safety. Even if elephants have no predators in IGR, humans might be associated with potential danger, as commonly reported for large herbivores (e.g., bison, Fortin and Andruskiw 2003; mule deer *Odocoileus hemionus* and pronghorn antelope *Antilocapra americana*, Taylor and Knight 2003), including elephants (Hunninck et al. 2017; Szott et al. 2019; Szott et al. 2020). A part of the IGR elephant population had experienced the culling operations in Kruger National Park before their introduction in the IGR. Thus, these elephants likely had a negative perception of humans (Ruinard et al. 2012). Vulnerability to predation is relatively high in cows with young, so females may be less inclined than males to visit areas considered risky (Chiyo et al. 2011). In contrast, males may be attracted to resources associated with infrastructure, such as green vegetation near tourist accommodation and staff houses, and water in gardens (Orrick 2018). Male elephants also mostly displayed higher relative probability of selection of areas close to roads than females (consistently with P₃), possibly reflecting sex differences in the trade-off between maintaining low levels of human activity and locomotion with high efficiency (Vanak et al. 2010; Tsalyuk et al. 2019). Roever et al. (2013) reported that selection varies between sexes and road types, with both sexes avoiding tarred roads, and males selecting secondary roads.

4.2. Density-dependent selection of habitat features detected during population growth

We showed that habitat selection of elephants varied with population density. Our analysis of density-dependence, however, has to be interpreted with caution because elephant density has increased steadily during the course of the study. It is therefore difficult to establish whether observed changes in selection were driven by conspecific density (e.g., increased competition), by the degradation of some cover types more than others, or by a gradual

habituation of individuals to human features proximity (e.g., Orrick 2018). That said, a growing number of conservation agencies rely on fences and enclosures to resolve human-wildlife conflicts (e.g., Mbaiwa and Mbaiwa 2006; Vanak et al. 2013; Pfeifer et al. 2014; Woodroffe et al. 2014). As megaherbivores such as elephants become increasingly confined to relatively small areas, their populations can grow and profoundly alter ecosystem functioning. The situation reported here thus reflects current and future conditions of many systems.

The covariation between animal density and time does not change the fact that density-dependent responses of elephants differed between sexes and seasons. We found that the relative probability of selection of areas near infrastructure increased with density for both males and females, especially in the dry season. Density-dependent effects on the selection of infrastructure were stronger for males than females. While the probability of selection of areas near roads increased with population size for both males and females in the wet season, males consistently selected areas close to roads more strongly than females throughout the year.

4.3. Management and conservation implications

Our study demonstrated that density-dependent habitat selection can explain growing concerns about elephant-human conflicts. Indeed, elephants typically increased their selection of human-related habitat features as their density increased. This aspect of habitat selection can be critical for accurate prediction of elephant distributions. A number of studies have underscored the risk of using habitat selection models to forecast animal distribution across different ecosystems or over time (e.g., Osko et al. 2004; Avgar et al. 2020). The poor predictive power of some models may reflect the lack of consideration of density-dependent changes in habitat selection (Avgar et al. 2020). Not only does our study consider such density dependence, but it goes further by using fine-scale habitat selection models to show that males and females can display different density-dependent responses to human-related habitat features. This demonstration is timely because there is increasing recognition that management interventions can have consequences that cascade across food webs, well beyond the target population or conflict area (Mbaiwa and Mbaiwa 2006; Osipova et al. 2018). Efforts to protect a given population may even conflict with the conservation objectives of other populations (Jordán and Báldi 2013; Sigaud et al. 2020). Accordingly,

there could be advantages to adopt practices that target specific individuals or areas, while minimizing the effect on others. We showed that the behavior of males makes them more prone to elephant-human conflicts than females, especially at high conspecific densities because they tended to visit the areas more frequently that are also used by humans. In the case of important human-elephant conflicts, lethal control or animal relocation could be used to target specific individuals (Treves et al. 2009). Various non-lethal approaches that can target specific individuals or areas are being developed, such as virtual fencing (Campbell et al. 2019), hazing (i.e. consistent aversive conditioning) (Petraçca et al. 2019), and repellents (Treves et al. 2009). Spatial modeling can then integrate these different measure to identify cost-effective solutions to mitigate human-wildlife conflicts, while also minimizing constraints on animal distribution dynamics (Fortin et al. 2020). Management actions can be implemented more effectively with knowledge of where, when, and on which segment of the wildlife population interventions should be targeted. Our study thus provides valuable information to implement such effective management planning.

CRedit authorship contribution statement

Daniel Fortin: Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. **Audrey-Jade Bérubé:** Conceptualization, Funding acquisition, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Stéphane Boudreau:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing. **Adrian Shrader:** Conceptualization, Data curation, Funding acquisition, Investigation, Project administration, Writing – review & editing. **David Ward:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Land cover types in Ithala Game Reserve

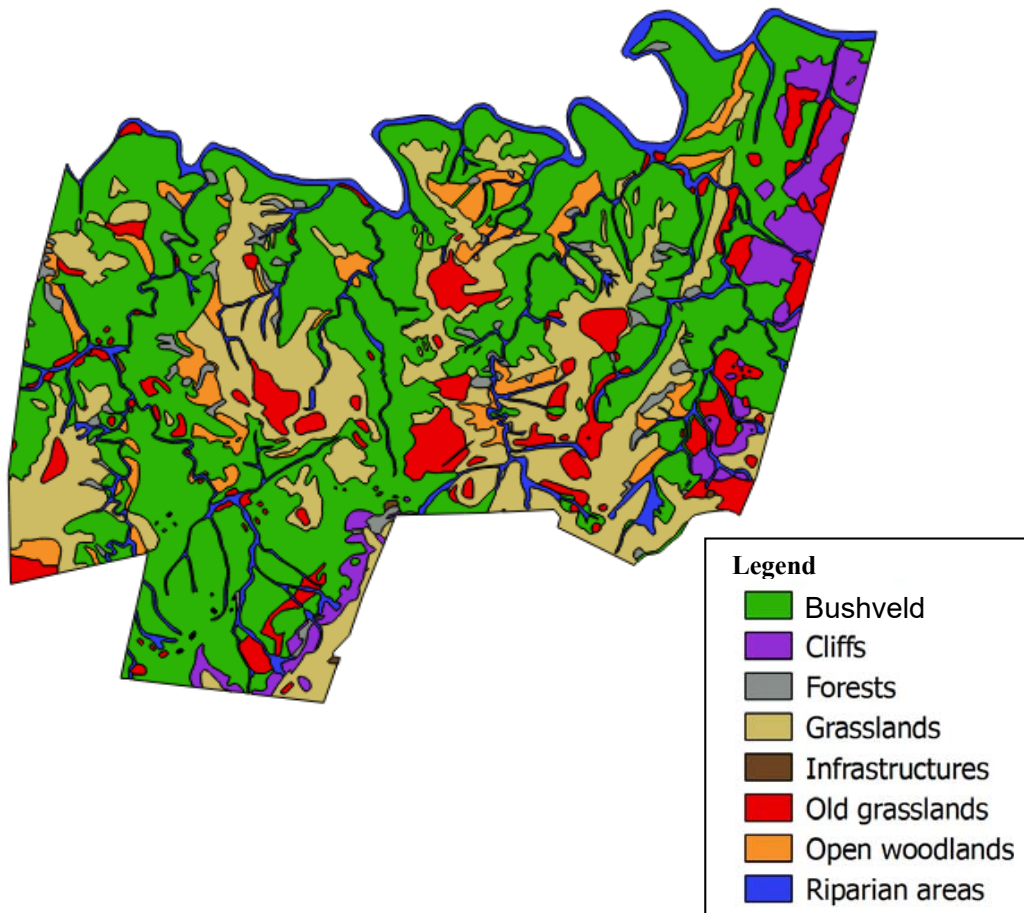


Fig. A.1. Distribution of the nine land cover types in Ithala Game Reserve, KwaZulu-Natal, South Africa.